WOODLAND SONG-BIRD POPULATIONS AND GROWTH OF NESTLING SPARROWHAWKS

DORIAN MOSS

Doctor of Philosophy

Department of Forestry and Natural Resources
University of Edinburgh

1976

ABSTRACT

Sparrowhawks prey largely on woodland song-birds. This study investigated the growth of nestlings in different environments, and song-bird populations in two areas between which Sparrowhawk breeding densities differed twelve-fold. The study areas were in Annan and Spey valleys, Scotland.

54 Sparrowhawk nests in Ae Forest and Annan valley, Dumfries-shire, were studied in three years. Weight, tarsus and primary lengths of nestlings were measured daily. Females rapidly grew heavier and larger, and in Ae Forest hatched sooner, than males. Mean growth rates of broods were independent of brood size, but decreased inversely with distance from good farmland. Hatching and growth rate orders were correlated. Wet weather depressed weight gain of nestlings. 21% of nestlings died, mainly in remote forest areas. Adult females were present less often at remote than valley nests. Development of sexual dimorphism, and the lack of relationship between brood size and growth rate, are discussed.

Literature on song-bird censusing is reviewed, and four methods selected for evaluation are described (mapping, simple and complex line transects, fixed-time counts). The 17 census plots were in plantations and semi-natural woods in the two areas. Results are compared and the methods discussed: mapping was found to be the most reliable method despite certain defects; densities from complex transects were inconsistent. The other methods were biased and did not give densities. Bird communities of the census plots are described. Diversities of bird species and foliage heights were highly correlated.

Prey samples at nest sites were biased, but contained many species. Abundant song-bird densities occurred only in some valley woods.

Sparrowhawks nesting in remote areas suffered nestling mortality and poor growth because local prey was scarce; and radio-telemetry showed that these birds commuted to the valley for prey. Song-bird densities in the best woods in the two areas differed four-fold; Sparrowhawk breeding densities twelve-fold.

CONTENTS.

CHAPTER 3 - SONG-BIRD CENSUSES Page 81

LIST OF TABLES.

LIST OF FIGURES.

CHAPTER 1

INTRODUCTION

1.1 Background

The Sparrowhawk Accipiter nisus is a small, broad-winged woodland raptor, whose prey consists almost entirely of birds. The species has a wide range in the Palearctic zone, which includes almost all of Europe and stretches across Asia, wherever there is woodland, to the Pacific (Brown & Amadon 1968). In Britain it was, until 1955, one of the commonest and most widespread birds of prey, despite persecution by gamekeepers over a long period. However from 1947 breeding success was reduced (Newton 1974), and in the late 1950s there was a marked decline in the population, so that in a survey conducted in 1963, Prestt (1965) found that it had almost disappeared from intensely arable areas such as lowland England and the central belt of Scotland, and had much declined elsewhere. Strong circumstantial evidence that these changes in population and breeding success were due to the use of toxic pesticides has been given by Ratcliffe (1970), Newton (1974), and Newton & Bogan (1974).

From 1947, when DDT was first used, Sparrowhawks started to lay thin-shelled eggs, which often broke, resulting in reduced breeding success. The substantial decline in the population however followed the introduction of the more toxic cyclodiene pesticides (aldrin, dieldrin and heptachlor) in 1955-6. Since 1962, when a voluntary partial ban on the use of the cyclodienes was introduced, the Sparrowhawk has made some recovery, particularly in the less intensively cultivated parts of Britain. Further restrictions on pesticide use have followed, with dieldrin banned from almost all uses from 1974. However Newton (1973a) found that breeding was still being

affected in 1971 by the persistence of residues in the environment and by continued use of pesticides, even in South-west Scotland, where the population suffered less severely in the 1950s than in eastern areas. Thus the Sparrowhawk has been found to be a useful 'environmental barometer', and in 1971 the Nature Conservancy (now the Institute of Terrestrial Ecology) initiated a programme of research aimed at investigating what factors limit Sparrowhawk numbers and breeding success in different areas, and particularly at assessing the continuing influence of organochlorine pesticides.

Some results of recent research have been published. Newton (1972a) gave data on the spacing of nest territories* in continuous forest in the Annan valley (Dumfries-shire) and Spey valley (Inverness-shire), showing that nest territories were regularly spaced in large tracts of woodland. In the two areas nest territories were on average 0.6 and 2.2 km respectively from their nearest neighbour, equivalent to densities of 2.5 and 0.2 nest territories per square kilometre respectively. These differences were consistent from year to year, but in neither area were all nest territories occupied in any one year, possibly because the population was to some extent still depleted.

Prior to 1971 there had been two major published studies of the Sparrowhawk. Owen (1915-1936) published a series of papers on observations of the birds, chiefly at nests. Although they contained some interesting material, particularly on breeding behaviour, these papers were not on the detailed scientific standard which is usual today. The classic study by Tinbergen (1946) from Holland contained details on numbers and densities, hunting methods, prey composition, and the effects of the Sparrowhawk on its prey populations. A more general

---

* A nest territory consists of an area occupied by a breeding pair. It may often contain old nests besides the nest in use at the time.

description of Sparrowhawk breeding biology was given by Newton (1973b), and other accounts included that of Kramer (1955).

1.2 Aims of the study

This study was centred on the factors affecting breeding density of Sparrowhawks and their success in rearing young, and in particular on the food supply available in different areas. The following question was asked: To what extent are the breeding density and the growth and survival of the nestlings correlated with prey abundance? This entailed not only a study of Sparrowhawks but also an investigation into what song-birds (the chief prey) are present and at what densities in different areas.

The first objective was to study the growth of young Sparrowhawks in a variety of local environments in Dumfries-shire, in order to investigate the extent to which differences in growth and survival of young occurred in different habitats, and whether these differences were related to differences in local prey abundance. This was achieved by taking daily measurements of the young in a number of nests throughout the nestling period. Thus the growth patterns, hitherto not recorded quantitatively, and the factors affecting success, could both be investigated, and are described in Chapter 2. This work complemented the more wide-ranging study of other aspects of Sparrowhawk breeding, which was simultaneously being conducted for the I.T.E. by Dr Ian Newton, part of whose study area was used.

The second question derived from the discovery (Newton 1972a) that Sparrowhawk densities in continuous woodland varied greatly between areas. The aim here was to investigate whether the breeding density in the predator was related to the breeding density of its prey. A programme of passerine bird censusing in woodland in the Dumfries-shire and Spey valley areas, where Sparrowhawk nest territories were 0.6 km and 2.2 km apart respectively, was therefore undertaken. In order to do this, several different census methods were

used and evaluated, with special regard to the requirement for consistency. This part of the project had the further objective of obtaining census data on the song-bird populations of modern conifer plantations, which have been neglected by ornithologists in past census work, but which now form a major habitat in upland Britain. The comparison of techniques and of the results obtained are described in Chapter 3.

The present study thus fitted into the I.T.E. programme of research on the Sparrowhawk, and involved four aspects of its ecology: the breeding density (already known); growth rates (this study); prey breeding densities (this study); and diet (data being collected by I. Newton, augmented in this study). The data on diet consisted of samples of prey gathered at nest sites, both on the nest and at nearby plucking posts.

1.3 The study areas

Figure 1 shows a map of the two areas inset on an outline of Scotland. Bird census work was undertaken in both areas, but Sparrowhawk nests were studied only in the southern one.

1.3.1 Dumfries-shire

The area can be divided into two parts (Figure 2). In the northern part the land falls from the Lowther Hills in the north (700-800 m above sea-level) to a series of broad ridges (300-400 m) which are drained by many steep-sided valleys. The southern part of the area consists of lowlands less than 100 m above sea-level, drained by the River Annan (which flows into the north coast of the Solway Firth), and its tributaries, the Kinnel and Ae Waters.

Much of the land above 150 m is of poor quality, and is mainly afforested; most of the remainder of the higher ground is open grassy sheepwalk. The largest forest in the area, the Forest of Ae, (55 km^2), was chosen for intensive study both of Sparrowhawks and of passerine bird densities. The forest is mostly 200-400 m above sea-level, and is planted both on the steep valley slopes and on the more level hill-top areas. The predominant tree species are Norway Spruce*, Sitka Spruce, and various larches. The trees were mainly planted in uniform stands, some of which have been opened up by wind damage. The wind-blown areas and some of the valley floors form the only breaks in the tree cover.

By contrast, the lowland supports a mixed landscape composed of good quality arable and pasture farmland, but broken by many small woods, plantations, and shelter-belts. The woodlands are of two main types: coniferous plantations of up to 2 km^2, where larch, spruces or

---

* Scientific names of all plant species mentioned are given in Appendix 2.

FIGURE 1 - OUTLINE MAP OF SCOTLAND SHOWING THE TWO STUDY AREAS (Figures 2 & 3)

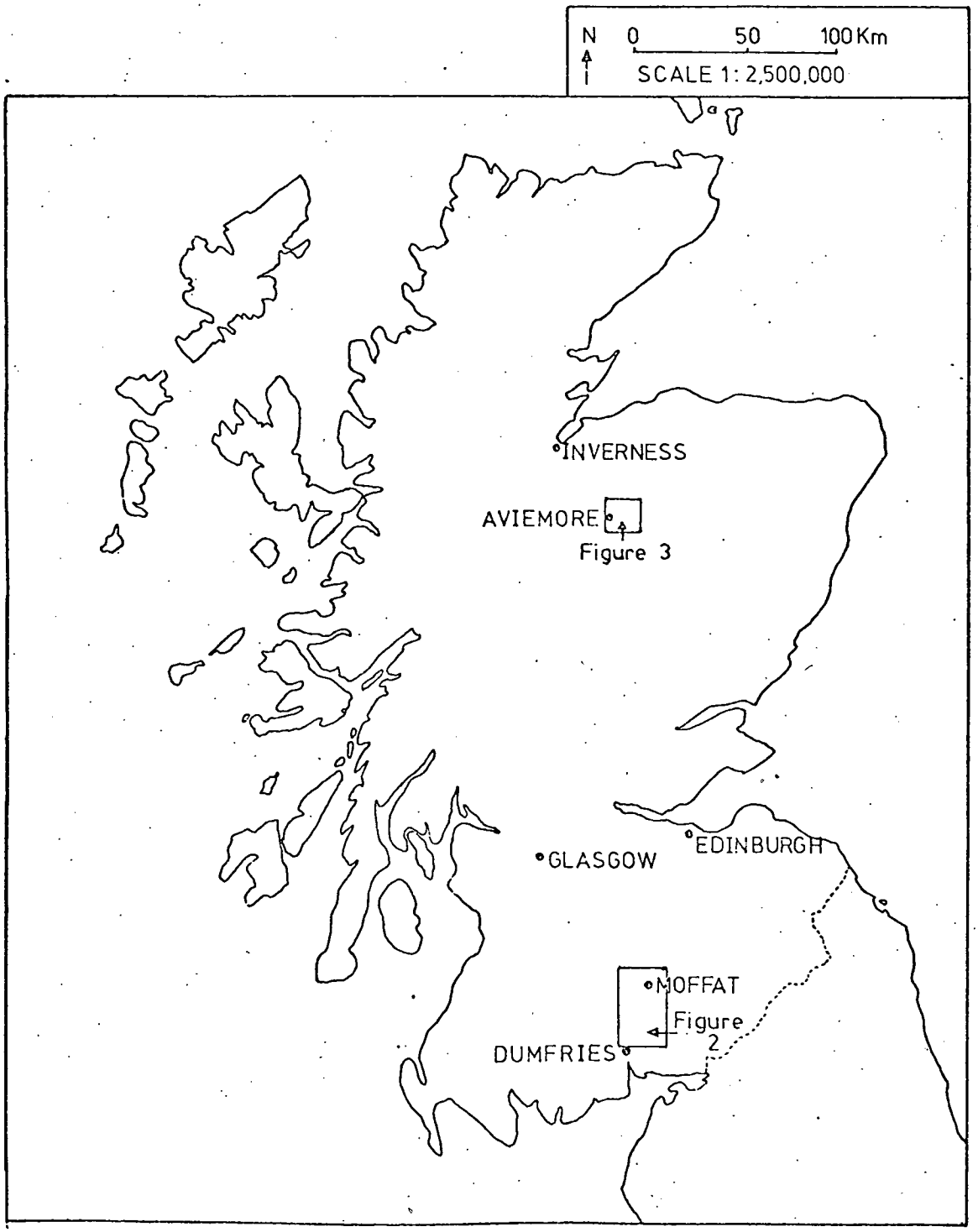
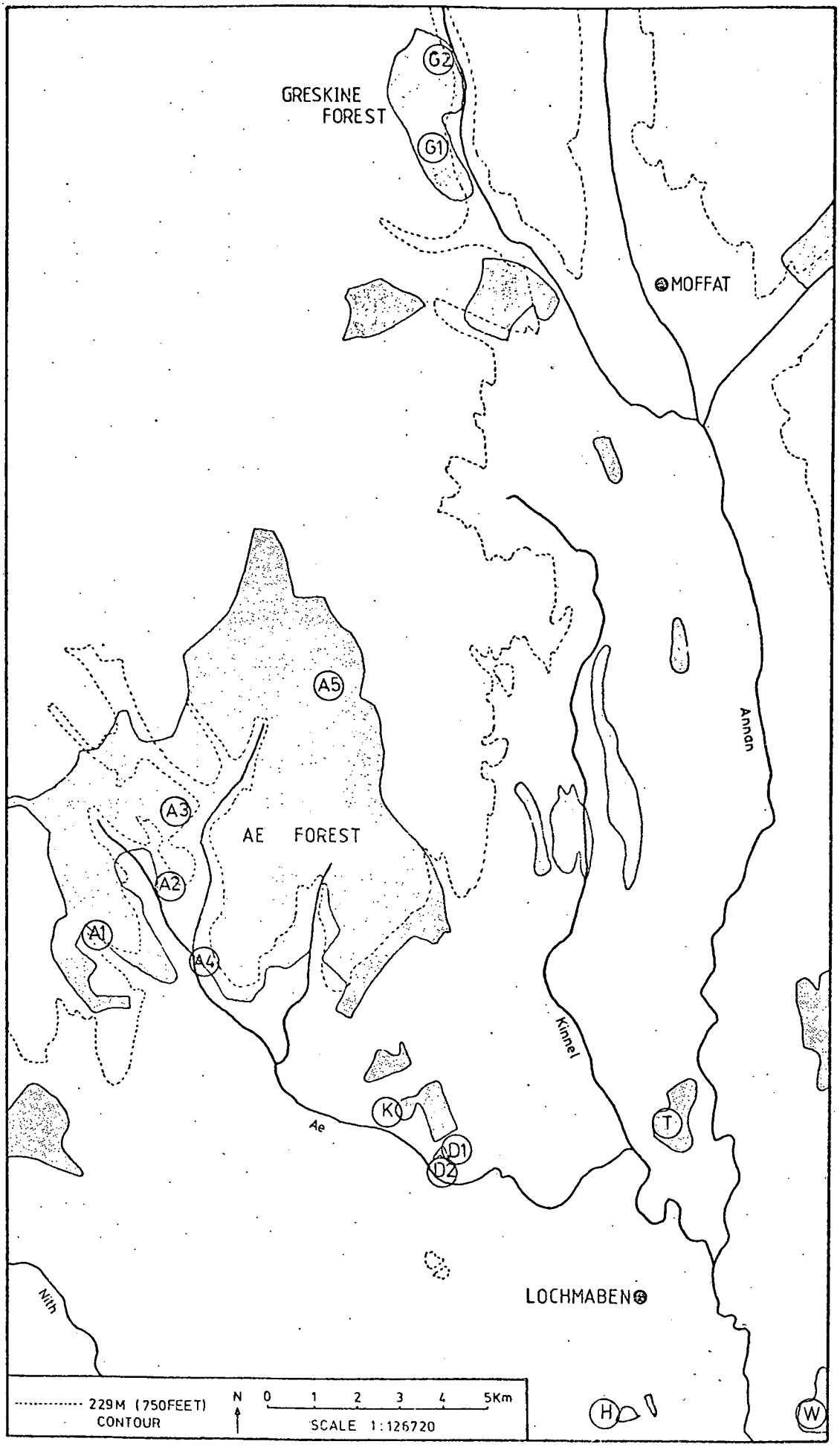


FIGURE 2 - MAP OF THE ANNAN VALLEY STUDY AREA, WITH WOODLAND AND THE CENSUS PLOTS MARKED



Scots Pine are planted; and older semi-natural woods, some of which are on disused peat cuttings, regenerating chiefly with pine, birch and heather.

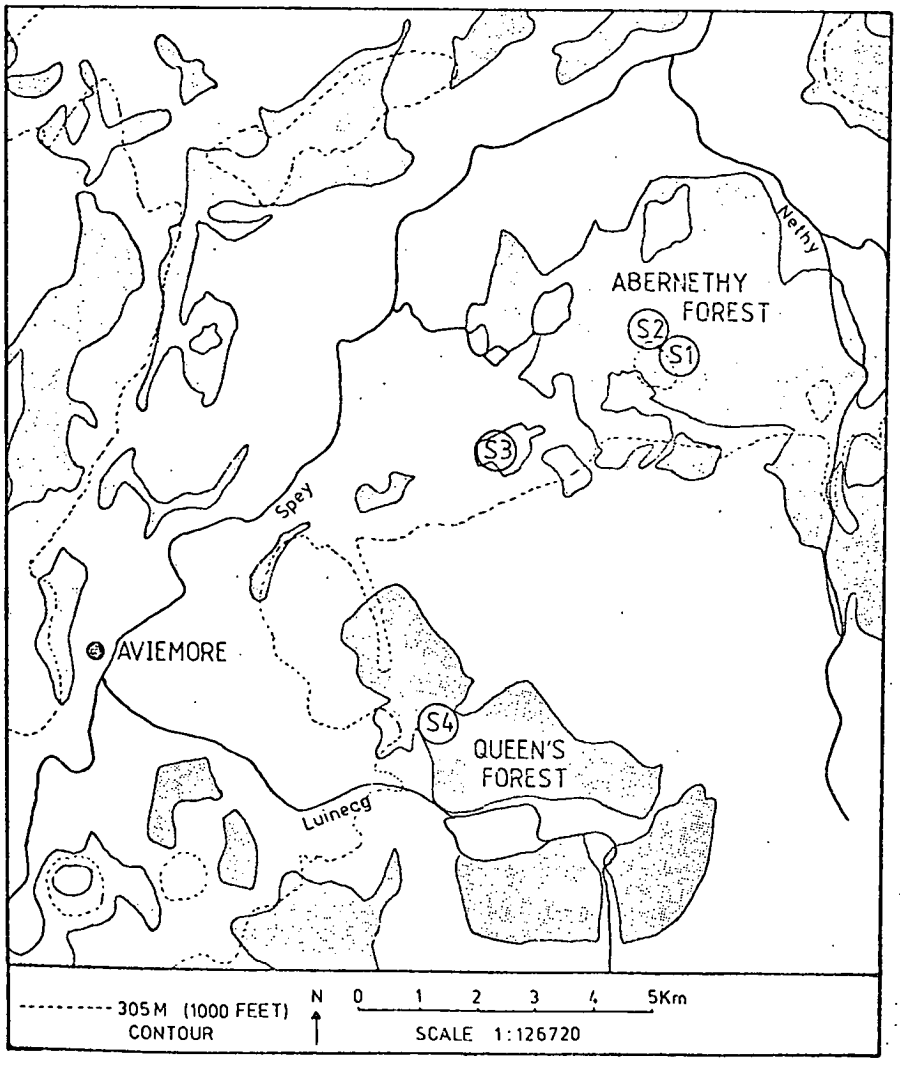
1.3.2 Spey valley

The River Spey flows north-eastwards through Inverness-shire in a valley averaging 5 km in width, between the Cairngorm and Monadhliath mountain ranges (Figure 3). The valley floor is flat, about 200 m above sea-level, with foothills of the Cairngorms rising to the south, eventually reaching summits of over 1200 m.

The main agricultural activity in the valley, where there is a narrow band of good quality land, is the raising of livestock. Grass is harvested in the summer for hay, but arable land is of very limited extent. The valley slopes, of poor land, are either used for forestry, or grouse moor, or they support semi-natural pine or birch woods.

The census plots studied in the Spey valley were in Abernethy and Queen's Forests. The former, an area of 24 km^2, contains a variety of woodland types, as well as open heather moor. The predominant tree species is Scots Pine - including remnants of the native forest - with smaller areas of birch. However planted pine predominates in the forest, as in the area as a whole. The Queen's Forest, in Glenmore (14 km^2), is mostly planted pine.

FIGURE 3 - MAP OF THE SPEY VALLEY STUDY AREA, WITH WOODLAND AND THE CENSUS PLOTS MARKED



CHAPTER 2

THE GROWTH OF NESTLING SPARROWHAWKS

The object of this part of the study was to collect information on the growth, mortality, and development of sexual dimorphism in nestling Sparrowhawks. Differences in growth rates were used in an investigation of factors which influenced growth and survival.

2.1 Published work on nestling growth, with particular reference to birds of prey

The literature on the growth of nestling birds, and in particular on their weights, encompasses a wide range of species, although several studies have been based on very few broods. Important contributions to the study of growth include those of Lack & Silva (1949) and Lees (1949) on the weights of Robins*, Harris (1966) on the growth of Manx Shearwaters, Maher (1964) on Snow Buntings and Lapland Buntings, Dawson & Evans (1957, 1960) on three Spizella species of American sparrow, and O'Connor (1975) on Blue Tit, House Martin and House Sparrow.

In a major review of patterns of weight gain in nestling birds, Ricklefs (1968) calculated growth parameters for over 100 species, making use to a large extent of data derived from the literature. He examined methods for computing rates of weight gain, and compared these rates both within and between species. In a further review, Ricklefs (1973) examined the relationship between the rate of weight gain in birds and the rate at which they reached maturity. Ricklefs' methods have however been criticised in another study of growth (O'Connor 1973), and were rejected for the purposes of comparison of growth in Sparrowhawks in the present study (p.29). Lack (1968) discussed the "growth rates" of many species and groups of birds, but

---

* Scientific names of all bird species mentioned are given in Appendix 1.

since he used this term to refer to the age at fledging rather than the quantitative rate of gain in any particular measurement, his treatment of growth did not have the scope of that by Ricklefs (1968, 1973).

Among the otherwise extensive literature, that on birds of prey is relatively scanty. Sumner (1929) made comparative studies of the growth of several species of raptor in the nest including one brood of Cooper's Hawk. However his sample sizes were very small, and measurements were made only at weekly intervals, so these observations were of limited value. In a later study, Sumner (1933) took nestling eagles and owls into captivity, and obtained daily growth data. He was able to describe the basic patterns of growth in this artificial situation. Watson (1957) studied the breeding biology of the Snowy Owl in Alaska. He obtained detailed data which showed that growth varied between the three broods studied intensively, and that the spread in growth rates within a brood was greatest when overall growth there was poor. In this situation the later hatched young grew more slowly than the earlier ones, roughly in order of hatching (which was spread such that in one brood 8 young hatched over a period of 12 days).

Schnell (1958) watched a single Goshawk nest in California. He described the development of the young and of their behaviour, and gave curves of weight gain in the three nestlings. A study of the Little Sparrowhawk by Liversidge (1962) was also made at a single nest, and included growth measurements made on the single nestling. Brown & Amadon (1968) devoted a short chapter of their review of the Falconiformes to a general discussion of the development of the young, including comparative growth data from five African species.

Only two published studies of growth in raptors which I have seen were on a large scale. Scharf & Balfour (1971) studied the growth

and development of Hen Harriers at 40 nests in Orkney. Measurements of weight and primary length were made at frequent intervals, although not daily. They found that adult female Hen Harriers were 50% heavier than adult males, but the authors did not publish separate mean growth curves for the two sexes, neither did they discuss in detail the development of sexual dimorphism. They found that within broods, growth rates differed irrespective of size-rank (the species is markedly asynchronous in hatching), but they failed to mention whether there were any differences in mean growth rates between broods.

Cavé (1968) made a detailed and comprehensive study of the breeding of the Kestrel on a reclaimed polder in the Netherlands. He included data on nestlings derived from 298 nests over five years. The birds nested in boxes erected in an area with few natural nesting sites. Daily weights of 17 nestlings from four broods were obtained, but the more usual measurement made was fledging weight. This was found to be independent of brood size, which ranged from two to six, but fledging weights of males were significantly reduced in one year when the food supply (voles) was scarce. Cavé also produced extensive data on mortality of nestlings, and related it to environmental conditions.

2.2 Field methods

The nests were built by the Sparrowhawks themselves, mostly in previously existing nest-territories, in March and April. All except two of the 54 nests studied were freshly built, the others being used in two consecutive years. All the nests except one were in coniferous trees of the various species available in the nest-territory. Nest sites tended typically to be in a position which allowed clear flight lines to and from the nest; in plantations they were usually close to a stream, track, or forestry extraction rack. Nest structure and position were not examined in detail, but have been studied by Hald-Mortensen (1974) in similar habitat in Denmark.

The nests were found each year by I. Newton and his helpers, as part of his study programme. He recorded laying dates and initial clutch sizes, and predicted approximate dates of hatching, based on an incubation period of 34 days. Almost all the clutches were started in May, and hatching dates ranged from 8 June to 11 July. Unlike many other birds of prey (including owls), Sparrowhawks did not begin incubation until the fourth egg was laid, so that hatching was relatively synchronous. My visits to the nests usually started 2-3 days before the predicted hatching date, and were made every two days until the first egg hatched, and daily thereafter. The eggs took up to two days to hatch from the time that they were first noticed to be chipping. In only a few cases the nest was not found until after the eggs had hatched.

In each year all the nests which were found in the Ae Forest were studied, and in addition an approximately equal number of nests in the Annan valley area were included for comparison (Table 1 and Figure 4). The Ae Forest was divided into three areas, referred to as remote,

TABLE 1 - LOCATIONS OF THE SPARROWHAWK NESTS STUDIED.

For an explanation of the areas see p. 50

	1973	1974	1975	Total
Ae Forest, remote	2	3	2	7
Ae Forest, central	4	3	4	11
Ae Forest, edge	3	3	3	9
Ae Forest, total	9	9	9	27
St Ann's	4	4	5	13
Templand	2	-	7	9
Annan valley total[1]	6	4	12	22
Moffat	1	4	-	5
Total	16	17	21	54

[1] St Ann's and Templand areas combined.

TABLE 2 - INCIDENCE OF BROODS WHERE EITHER (a) THE ENTIRE CLUTCH/BROOD OR (b) UP TO TWO NESTLINGS WERE ARTIFICIALLY INTRODUCED, AND (c) THE NUMBER OF 'NATURAL' BROODS.

	1973			1974			1975			Total		
	a	b	c	a	b	c	a	b	c	a	b	c
Ae Forest, remote	1	-	1	1	-	2	-	1	1	2	1	4
Ae Forest, central	2	1	1	1	-	2	1	-	3	4	1	6
Ae Forest, edge	1	-	2	1	2	-	1	-	2	3	2	4
St Ann's	-	-	4	-	-	4	-	-	5	-	-	13
Templand	1	-	1	-	-	-	-	-	3	1	4	4
Moffat	-	-	1	-	1	3	-	-	-	-	1	4
Ae Forest, total	4	1	4	3	2	4	2	1	6	9	4	14
Annan valley, total	1	-	5	-	-	4	-	4	8	1	4	17
Total	5	1	10	3	3	11	2	5	14	10	9	35

central, and edge, for comparative purposes. The positions of the dividing lines (Figure 4) will be explained later (p.50). The Annan valley was also divided into three areas: Templand, St Ann's, and Moffat. The first two of these, which did not differ in habitat structure, will be referred to together as "Annan valley".

At least 12 consecutive days' data were obtained for a total of 54 nests, of which 47 were studied for at least 19 consecutive days. Of the remaining 7 nests, one was not found until the young were ten days old, and at the other six, all the nestlings died between 12 and 18 days old.

In a number of cases, eggs or newly hatched nestlings were transferred between nests, in order to maximise the number of broods available within the study area, particularly in the Ae Forest. Small broods of one or two nestlings were also augmented with additional nestlings, because it was thought that such broods could otherwise have been raised easily at any site, and so would not have produced information on growth rate in relation to the site quality. Most of the transfers followed the breakage of eggs during incubation, a phenomenon which is almost certainly due to a reduction in eggshell thickness and to abnormal behaviour in the hen as a result of organochlorine pesticides (Newton 1974). The resulting small broods soon after hatching are therefore not natural. Nests were checked every five or six days during incubation, and any eggs which had disappeared were replaced with artificial dummies, which were readily accepted by the incubating birds. When whole clutches had been replaced by dummies, these were in turn replaced by hatching eggs or newly hatched nestlings from outside the study area, when these became available. The replacements were accepted as if they had hatched naturally, and provided ten broods for study at sites which would otherwise have

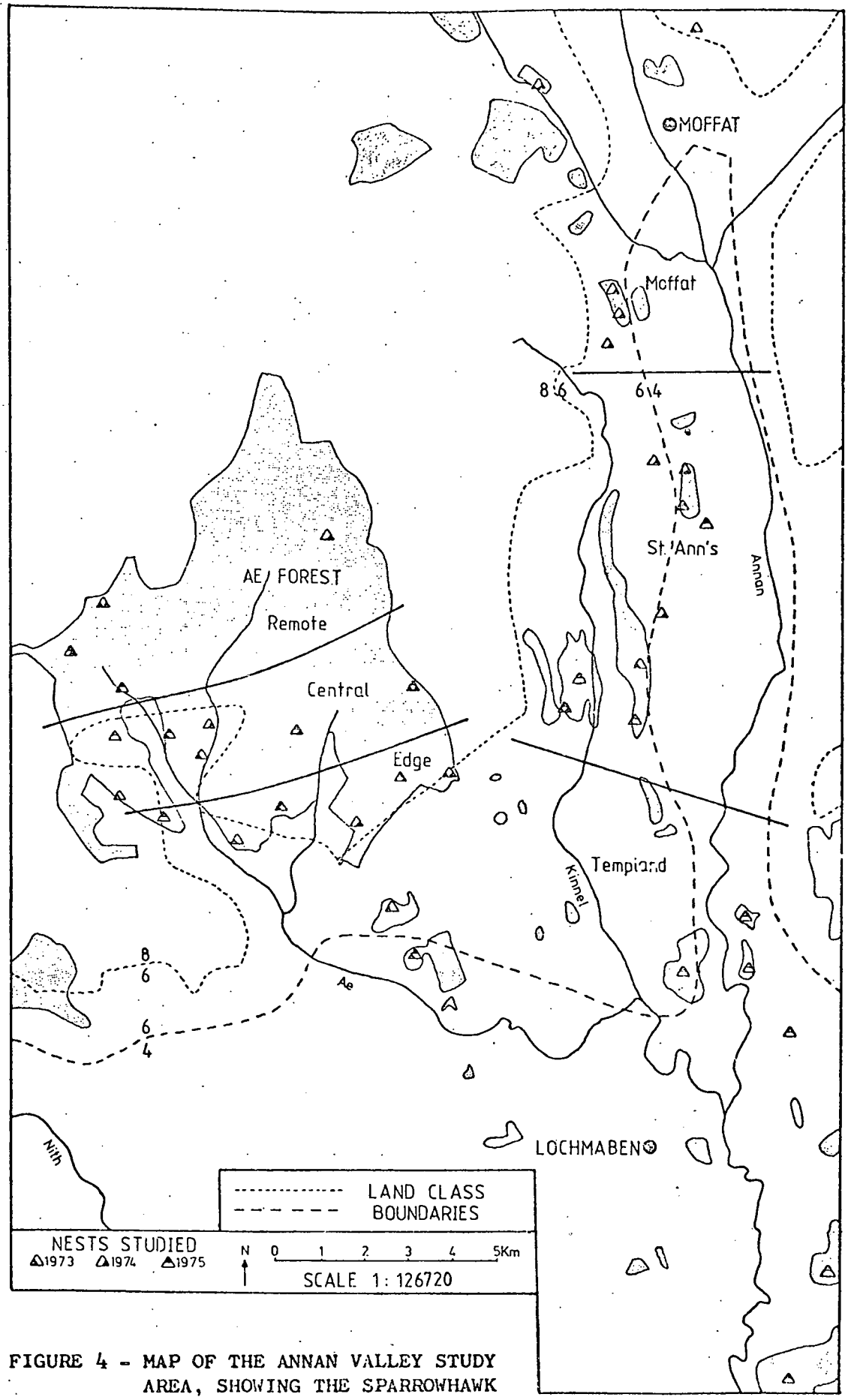


FIGURE 4 - MAP OF THE ANNAN VALLEY STUDY AREA, SHOWING THE SPARROWHAWK NESTS STUDIED IN EACH YEAR, THE PRINCIPAL LAND CLASSES, AND THE SUB-AREAS INTO WHICH THE AREA WAS DIVIDED

failed during incubation (Table 2). Partially broken clutches were made up to normal brood sizes on hatching by the addition from elsewhere of compatible nestlings which were no more than one day different in age from those hatched naturally. The same procedure was followed when eggs failed to hatch after the full incubation period, and these eggs were taken for analysis (Newton & Bogan 1974). In 1975 nestlings were also added to nests when necessary in order to raise each brood size to four, so as to compare growth rates and mortality between broods of at least this size.

Although the presence of organochlorine pesticides affected the eggs and incubation behaviour of some of the birds, there was no evidence that it had any effect on the growth and survival of nestlings after hatching. Newton (pers. comm.) noted a number of Sparrowhawk nests in which the young were reared successfully, yet any unhatched eggs of the clutch contained high pesticide levels. When complete clutches were analysed, all the eggs contained similar pesticide residue levels to each other, so the young mentioned above would have hatched from highly contaminated eggs.

Over the three years, as well as the ten replacements of entire clutches, up to two nestlings were added at a further nine nests (Table 2). There were four other transfers of young between study nests: in 1973, two 15-day-old nestlings were found below a nest in Ae Forest where the third had been taken by a Tawny Owl, and were placed in other nests; and in 1975, two 7-day-old nestlings were exchanged in connection with another project.

Each nestling was individually marked on the head with a coloured felt marker pen on the first day when it was seen, so that it could be identified thereafter. The marks were renewed when they became faint,

about every ten days, until the young were ringed. On each visit, four measurements were made of each nestling:

1) Tarsus length (to the nearest 1 mm): to measure the rate of bone growth. Measured with calipers from above the ankle joint to below the point where the toes diverged.

2) Outermost primary feather length (1 mm): to measure the rate of feather growth. The measurement was taken from the skin and included the sheath as well as the feather vane. The outermost primary was chosen because it could be measured quickly without error, and, since the Sparrowhawk is round-winged, the outermost primary is only a little shorter than the longest primary.

3) Weight (1 g): to measure overall growth of the bird. Weight was likely to be the best indicator of differences in growth rates of nestlings caused by food supply, parental care, and bad weather. Measured with a Pesola spring balance, 100 g or 300 g capacity as appropriate.

4) State of the crop. Food in the crop could be felt through the skin, and was judged on a scale of quarters from zero (empty) to one (full). The crop state was noted so as to detect whether the nestling had been fed recently before the visit.

In addition, on each nest visit I noted whether the adult female was present or not. In the third year, when I had noticed consistent differences in the females' behaviour in the earlier years, I also classified the behaviour according to the intensity and frequency of the female's calls as "agitated" or "not agitated". The time was also noted, and whenever possible I made the visits to each nest at approximately the same time each day, so that measurements could be made every 24 hours.

Nest visits were made daily from hatching until the nestlings were 22-25 days old*, when visits stopped to avoid the possibility of fledglings leaving the nest prematurely. On the few occasions when young did leave the nest, they were recaptured and replaced. It was not possible to measure the effects of my disturbance upon the growth of the nestlings; however it was unlikely that I caused the two cases of desertion, and other effects of disturbance would have been the same at every nest studied. Nestlings which were handled every day were much less likely to leave the nest prematurely at 21-25 days old than nestlings which were handled for the first time at that age (for ringing). Lack & Silva (1949) found the same tolerance in Robins which they weighed daily compared with other nestling Robins.

---

* References later (for example sections 2.9 and 2.10) to "fledging" and "24 days" refer to the last visit made, when the nestlings were 20-24 days old (20-21 day-old nestlings on these occasions being those which were the last hatched). Little information was gathered for nestlings over 24 days old, and this was not used.

2.3 Development of the nestlings - qualitative description

Notes were made on the age at which various characteristics appeared, in particular the feather tracts, and also on behaviour (Table 3). The important point is that in the development of plumage and of abilities such as standing on tarsi and perching on branches, male nestlings were about two days ahead of females.

TABLE 3 - DEVELOPMENT OF FEATHERS, BEHAVIOUR, AND OTHER FEATURES IN NESTLING SPARROWHAWKS.

Feeding observations were made from hides by Mulliner & Reeves (1974).

Age (days)	Feather development	Behaviour	Other features
0	Covered with translucent down, appearing pinkish.	Quiet peeping calls.	Cere and legs pink. Eyes blackish brown, open soon after hatching.
4		Snatch food from female, little competition.	
5	Primary sheaths appear.	Chirping calls. Beg from observer from 2-12 days when hungry.	
9	Secondary and tail sheaths appear.	Peck at prey without success.	Cere pale straw, legs straw.
10	Primary covert and scapular sheaths appear.	First calls resembling adults'.	
11	Primary vanes appear.		
12	Secondary and covert vanes appear.	First aggression towards observer.	Down on lores wearing off.
13	Thick greyish-white second down. Vanes of tail appear.	Pull off a little meat from prey.	
14	Scapular vanes. First body feathers, on flanks.	Can pick at food but unable to feed successfully.	
15		Male standing on tarsi.	
16	Vanes of tail coverts appear.		Lores bare. Eyes dark olive-brown.
17		Female standing on tarsi.	Cere lemon-yellow, legs becoming yellowish.

TABLE 3 (continued)

Age (days)	Feather development	Behaviour	Other features
18	Scapulars form stripes down back. Shoulder and flank body feathers.	Loud and frequent calls like adults' alarm during nest visits, esp. from males.	
19		Able to eat complete prey, but very inefficient.	
20	Scapulars, back and flanks feathered; males more advanced than females.	Male perching on a branch by nest.	Eyes yellowish-grey.
22	Male crown feathers.		
24		Male may leave nest prematurely.	
26		Female may leave nest prematurely.	
24 (male)))	Down remains on upper and under sides of tail coverts, on centre of belly, on crown and amidst wing-coverts. Back chestnut with paler tips, breast barred and blotched with chestnut.	Able to tear up prey almost as fast as adults.	Eyes grey-yellow.
26 (female))			

2.4 Treatment of the growth data

Nestlings which were not measured from the day of hatching (just over a quarter of the total sample), were aged by their first tarsus measurements, on comparison with the tarsus lengths of birds of known age. The tarsus length was chosen for this purpose because it was less variable than weight. All nestlings could be sexed at the age of 16 days by the greater weight, tarsus length and tarsus diameter of females. All the young which survived to 16 days were sexed, and so were some of those which died earlier, if their measurements were close to the pattern of one or other sex. The 54 nests studied contained a total of 215 nestlings which survived for at least two days: 95 males, 105 females, and 15 unsexed.

The growth data for each nestling were stored in a file of a digital computer, and a number of programmes was developed to analyse them. These included calculation of age-specific mean values of each measurement for both sexes; growth rates over standard age ranges; mean growth rates at each nest; and regression of growth rates against a number of environmental and other factors.

The mean growth curves (Figures 5-7) were obtained from the total sample of normally growing nestlings; that is all birds except runts, which were smaller than their siblings from an early age and eventually died. Measurements of previously normal birds which went into an irreversible decline and then died were excluded after the start of the decline.

Weight increased slowly for 4-6 days from hatching, then increased rapidly for 10 days, and later again increased slowly, sometimes with marked fluctuations. Sumner (1933) recognised a similar three-stage process in raptor weights; and Ricklefs (1968) compared data from a

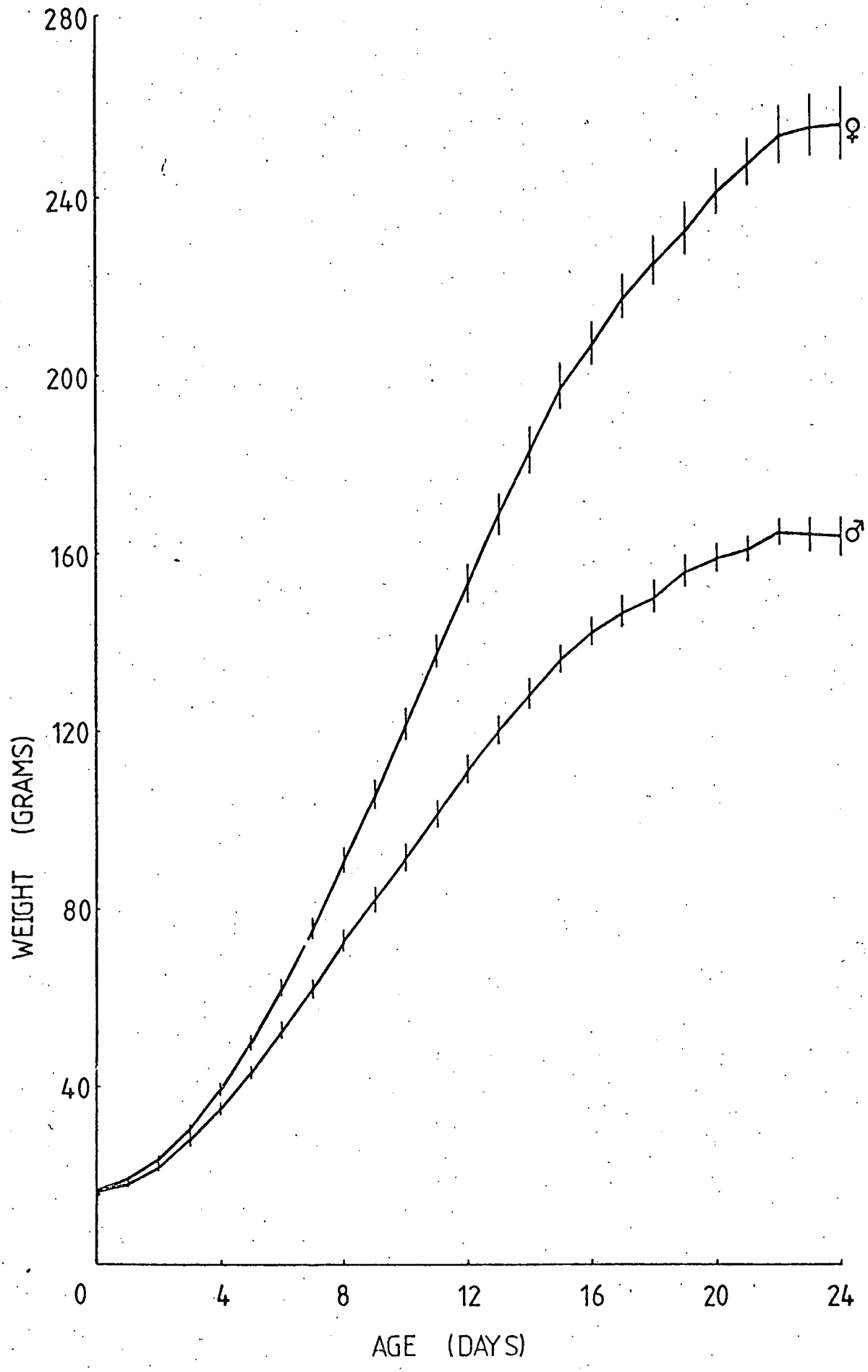


FIGURE 5 - MEAN WEIGHTS OF NESTLING SPARROWHAWKS, WITH 95% CONFIDENCE INTERVALS FOR EACH SEX

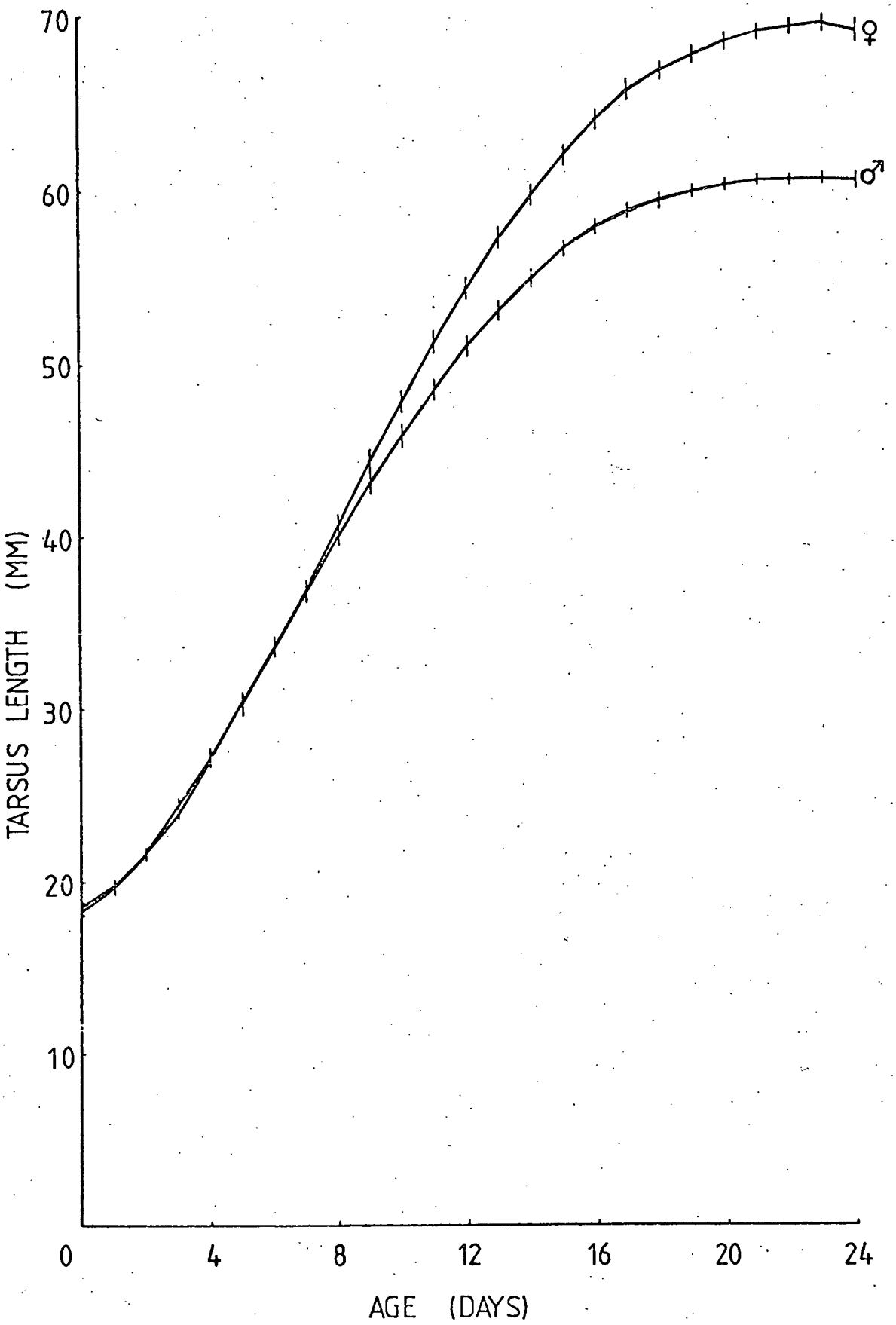


FIGURE 6 - MEAN TARSUS LENGTHS OF NESTLING SPARROWHAWKS, WITH 95% CONFIDENCE INTERVALS FOR EACH SEX

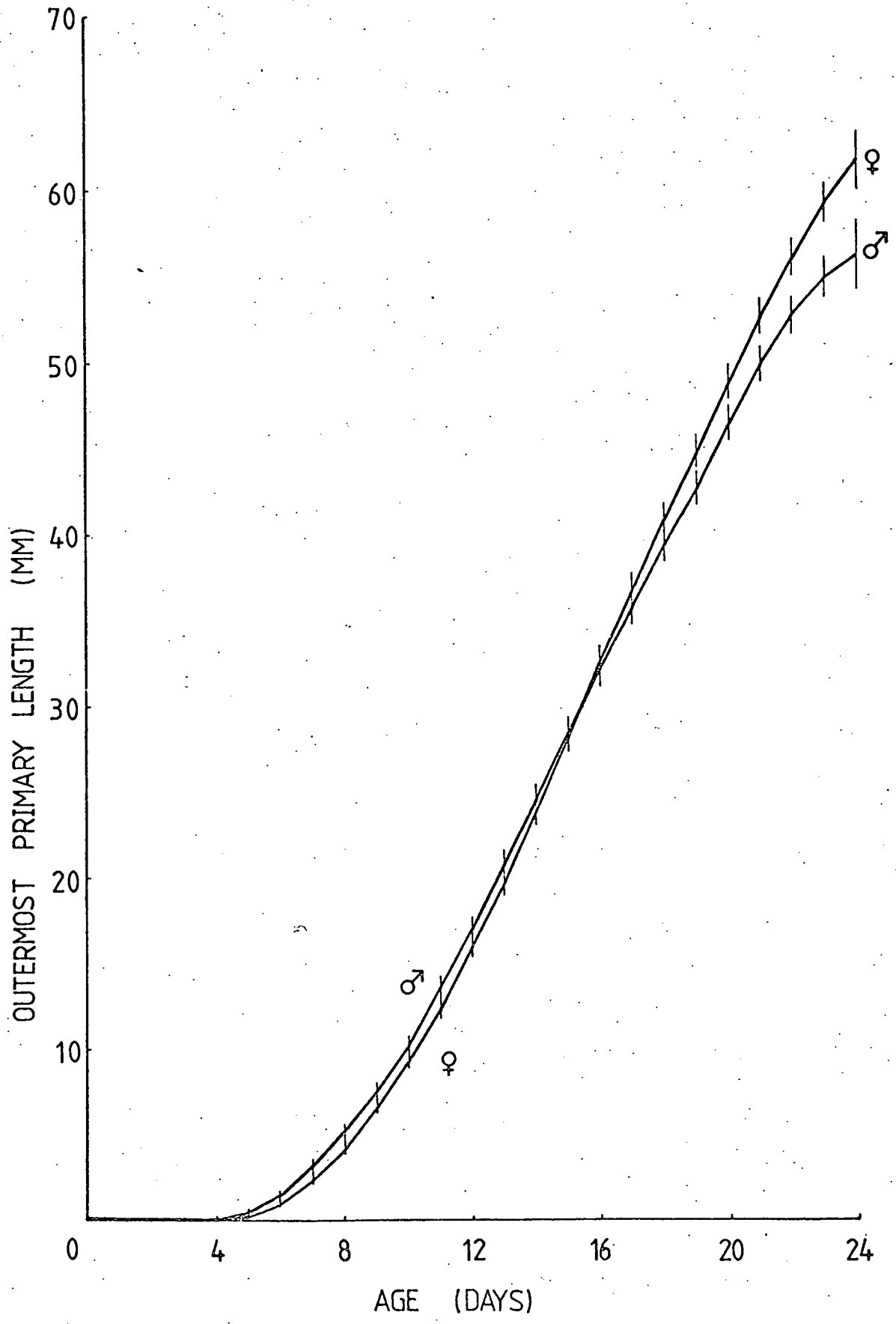


FIGURE 7 - MEAN OUTERMOST PRIMARY LENGTHS OF NESTLING SPARROWHAWKS, WITH 95% CONFIDENCE INTERVALS FOR EACH SEX

wide range of species, all of which conformed to the same inherent pattern. The curves were thus basically sigmoid in shape, although those for tarsus length were truncated at the left-hand end, and those for length of primary feather at the right-hand end. The central part of each curve was essentially linear. The periods of linear growth were found, and linear regression coefficients were calculated over these periods for each nestling. Fresh graphs were drawn of the mean measurements of ten nestlings of each sex which had the highest growth rates, and from these graphs the periods of linear growth of the fastest growing young were determined. These periods, which were all of at least nine days (Table 4), were used as standards in all further growth rate calculations.

Growth periods were chosen in this way in order to maximise the differences between birds which grew fast but completed their growth early, and those that grew more slowly for a longer period. It was expected that growth differences at this stage would reflect differences in food intake between broods. The standard error of each growth rate was equal to the standard error of the linear regression coefficient.

Growth rates were calculated for 188 nestlings from 52 broods for weight and tarsus length, and for 178 nestlings from 49 broods for outermost primary length. Runts were excluded because some of them died before full growth data had been obtained from them, and also so as not to bias the mean rates of growth at nests which otherwise contained healthy nestlings. Each growth rate was also expressed as a percentage of the mean growth rate of the total sample of each sex, so that birds of either sex could be compared directly, and so that growth rates of birds of both sexes could be used to obtain means for each nest.

The method of Ricklefs (1967) for fitting non-linear functions to growth data was only applied to the overall mean values. This method required the estimation of an asymptote for each measurement, that is the final plateau value to be reached in the sigmoid curve plotted against age. In the case of weight (the most important measurement made and the only one studied by Ricklefs), there was considerable variation in weights of individual Sparrowhawks beyond the age of 18 days, and individual asymptotic weights could not be found for many of the nestlings. For the mean values of all males and all females, the asymptotes (a) were 165 and 255 grams respectively, and the values of the growth coefficient k in the equation $w = a/(1+e^{-k(t-t')})$ were 0.257 and 0.262 respectively, where w = weight, t = age, t' = age when weight = $\frac{1}{2}a$. This result, with no difference in growth rates of Sparrowhawks between the sexes, was in contrast to that of Ricklefs (1968), who found a 40% higher rate in the male than in the female of the closely related Cooper's Hawk. His data were taken from a very small sample of four males and one female published by Sumner (1929), and were consequently of limited value.

To summarise, linear regression was used in preference to Ricklefs' method because:

(1) It was difficult to find asymptotic weights for individuals;

(2) Ricklefs' method gave two values (asymptote and growth rate) which would complicate comparisons between groups of birds;

(3) The method of using linear regression coefficients could be applied over a sufficiently long period, was simple to calculate consistently, and provided ready comparisons between birds. Birds of either sex could be compared when the

growth rates were standardised to percentages of the means for each sex.

Part of the weight of each nestling was due to food in the crop, whose fullness was recorded together with weight. Some of the day-to-day variations in weight away from a linear gain could be ascribed to variations in the amount of food in the crop, and a program was developed to determine the growth rate when these variations had been accounted for. To simplify the computation, it was assumed that the capacity of the crop grew as the bird grew, so that the weight of food due to a full crop was a fixed percentage (R) of total body weight, irrespective of age, and that the weight of food in a crop recorded as a fraction of full varied pro-rata.

For each bird a value of R was determined which minimised the coefficient of variation of the regression coefficient of weight when reduced by R% X the crop fraction. The mean values of R were 8.4 ± 4.4 (N = 89) for males, and 8.2 ± 4.1 (N = 104) for females. There was no difference between the sexes, and over 50% of values lay between R = 5% and R = 11% inclusive.

This correction for crop was not used further, because I thought it likely that the birds with highest growth rates would have been fed more often, and so have had fuller crops, than those with low growth rates. A reduction to correct for the amount of food in the crop would thus have introduced a bias in growth rate against the better fed, and so faster growing, birds. It was not possible to test for a correlation between the average crop 'score' and growth rate, because the crop score also depended on the time of day when measurements were taken. Since each nest was visited at approximately the same time each day, the three variables (crop score, time of day, and growth rate) could not be separated so as to analyse the relationship between any two of them.

2.5 Characteristics of nestling growth

As in other species of raptorial birds (Brown & Amadon 1968), the nestling period was divided such that bone growth was almost complete half-way through the period, and weight stopped increasing rapidly at about the same time, while feather growth took place during the second half of the nestling period (Figures 5-7).

Adult female Sparrowhawks are about 100% heavier than adult males, with 15% longer tarsi and 15% longer wings. The differences in weight became apparent at an early stage after hatching, so that although there was no overall difference on the day of hatching, females were significantly heavier than males ($P < .05$) when one day old (Figure 5). (They were sexed retrospectively.) The equivalent ages for tarsus and outermost primary lengths were 9 and 18 days respectively. At the earlier stages there was no significant difference between the sexes in tarsus length (Figure 6), but the males' primary lengths were significantly greater than the females' from age 6 to 13 days (Figure 7).

I noticed during the 1973 season that the first bird of a brood to hatch was a female in almost every nest, which suggested that eggs producing females tended to have a shorter incubation period than those producing males. This suspicion was tested over three years as follows: in every brood where both sexes were found and individual hatching dates were known, the mean hatching date of birds of each sex was calculated. The numbers of broods with mean hatching date of females before that of males, and *vice versa* were counted. Only naturally hatched broods were included when each area was considered separately, but one complete clutch brought from elsewhere to the Ae Forest was included in each year's total (Table 5). The one-tailed

TABLE 4 - PERIODS OF LINEAR GROWTH USED IN THE GROWTH RATE CALCULATIONS. Ages in days.

	Weight	Tarsus	Outermost primary
Males	4 - 14	2 - 10	10 - 20
Females	6 - 15	3 - 13	11 - 19

TABLE 5 - SEX DIFFERENCES IN HATCHING DATE WITHIN BROODS.

Year	Area	Number of broods with: Mean♀ < mean♂	Mean♂ < mean♀	Probability[1]
1973	Ae Forest[2]	3	0	0.125
	Annan valley[2]	0	0	-
	Total[3]	5	0	0.031
1974	Ae Forest	4	1	0.188
	Annan valley	1	2	-
	Total	8	3	0.113
1975	Ae Forest	4	1	0.188
	Annan valley	5	5	0.623
	Total	10	6	0.227
All	Ae Forest	11	2	0.011
	Annan valley	6	7	0.709
	Total	23	9	0.025

[1] One-tailed probability using the binomial distribution of a result at least as extreme under the null hypothesis that either case was equally likely.

[2] 'Natural' broods only.

[3] Total = Ae Forest + Annan valley + Moffat area + complete clutches transferred from elsewhere.

probability of a distribution as extreme (towards earliness in the females) as that observed was calculated using a binomial distribution, under the null hypothesis that either case was equally likely. The results were sub-divided by areas and by years (Table 5). There was a marked difference between Ae Forest and Annan valley: the result for Ae Forest was significant (P = .011), but in the valley the two categories were observed equally often. The overall total was also significant (P = .025), and so was that for 1973 (P = .031). In each year there was a strong tendency towards earlier hatching of females in the forest, but the sample sizes were too small for significance.

Assuming no sex differences in order of laying, then in one area, but not in the other, eggs producing females had slightly shorter incubation periods than those producing males, which resulted in the effect found in hatching order. Female nestlings were the same weight as males on the day of hatching, but were significantly heavier when one day old, as mentioned above, and the weights continued to diverge thereafter. It would be expected that female nestlings took more food than their male siblings, either by begging more successfully, or for longer, from the adult hen at each feed, and that being hatched first would be advantageous to them in achieving superiority in the brood. However studies from hides at nests showed that both sexes received approximately the same number of mouthfuls of food during each stage of the nestling period (Mulliner & Reeves 1974, Moss M. 1975). The process whereby the females increased their weights markedly over the males was probably coupled with the tendency for males to expend relatively more energy in developing feathers and various capabilities before the females (Table 3), and possibly also due to higher metabolic rates in the males.

The period taken for a clutch to hatch increased with clutch size, as might have been expected. For the 44 natural broods for which hatching dates were known, the number of days between the hatching of the first and the last egg was found, and compared according to clutch and brood size (Figure 8). The majority of broods took one to two days to hatch. Since in 21 of these 44 cases not all the eggs hatched, the results differed according to whether clutch or brood size was used, but both sets were biased in the measurement of true hatching spread in the ideal situation of a 100% hatch. The classification by clutch size under-estimated the hatching spreads, which would have been greater had all the eggs hatched, while that by brood size gave over-estimates, because the spread would have been less had only the number of eggs which hatched been laid. Thus in each case (Figure 8) the mean hatching spread based on brood size was higher than that based on clutch size. Apart from the brood size of two, based on a very small sample, the mean hatching spread increased regularly with clutch and brood size, and the difference between broods of three and broods of four and five combined was significant ($t = 2.63$, 38 d.f., $P < .02$).

The variation in weight and tarsus length between individuals was examined with respect to age by plotting the coefficients of variation (standard deviation X 100 / mean) for each measurement and both sexes against age (Figure 9). The greatest individual variation in every case, 50-80% higher than at age zero, occurred between three and five days, and it fell steadily thereafter to 25-55% of the peak value. There was more variation between females than between males. These results imply that the differences in individual growth rates, to be described in detail later, appeared at an early stage of development,

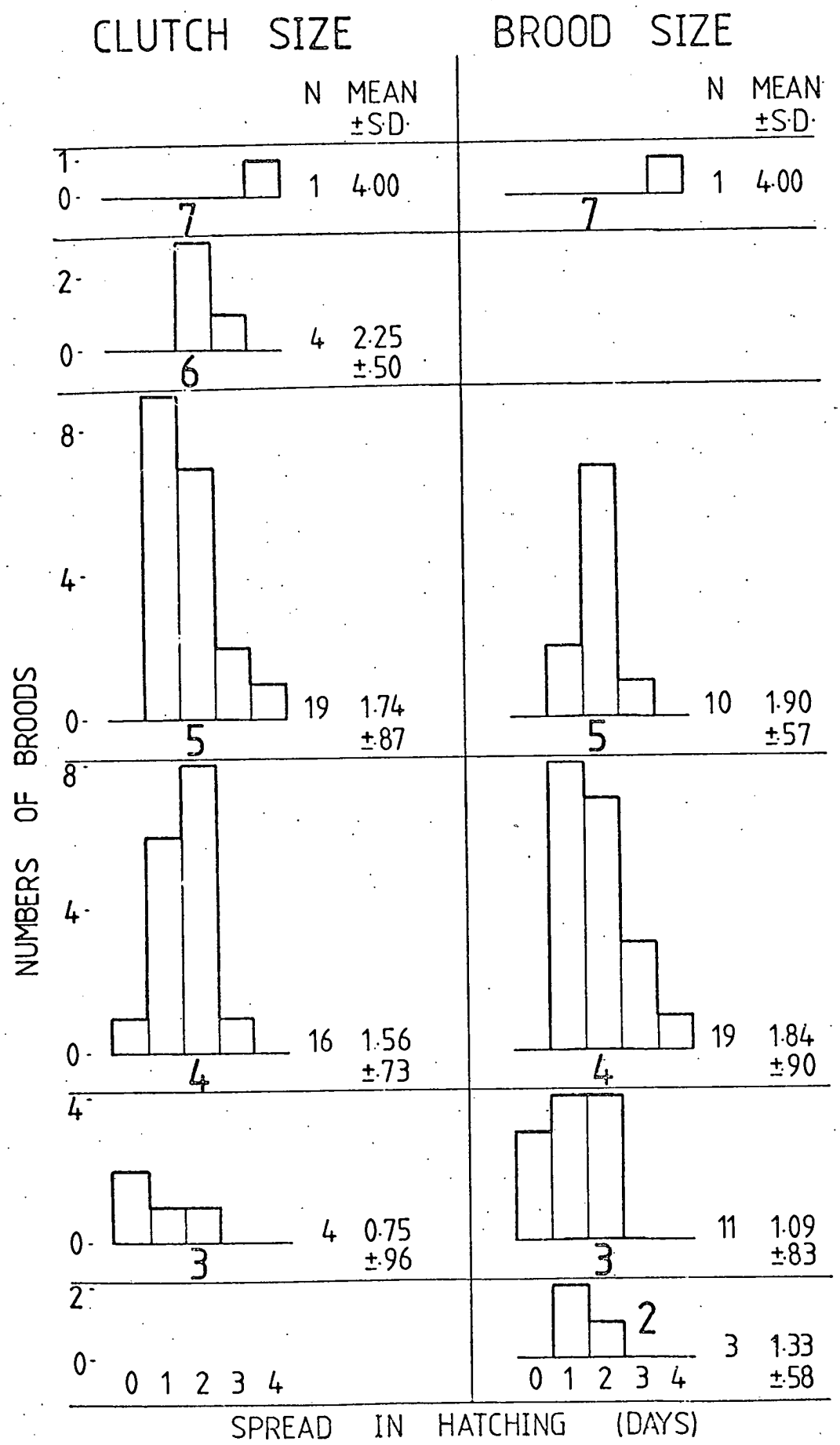


FIGURE 8 - THE SPREAD OF HATCHING IN BROODS OF DIFFERENT SIZES, CLASSIFIED ACCORDING TO CLUTCH SIZE AND TO BROOD SIZE

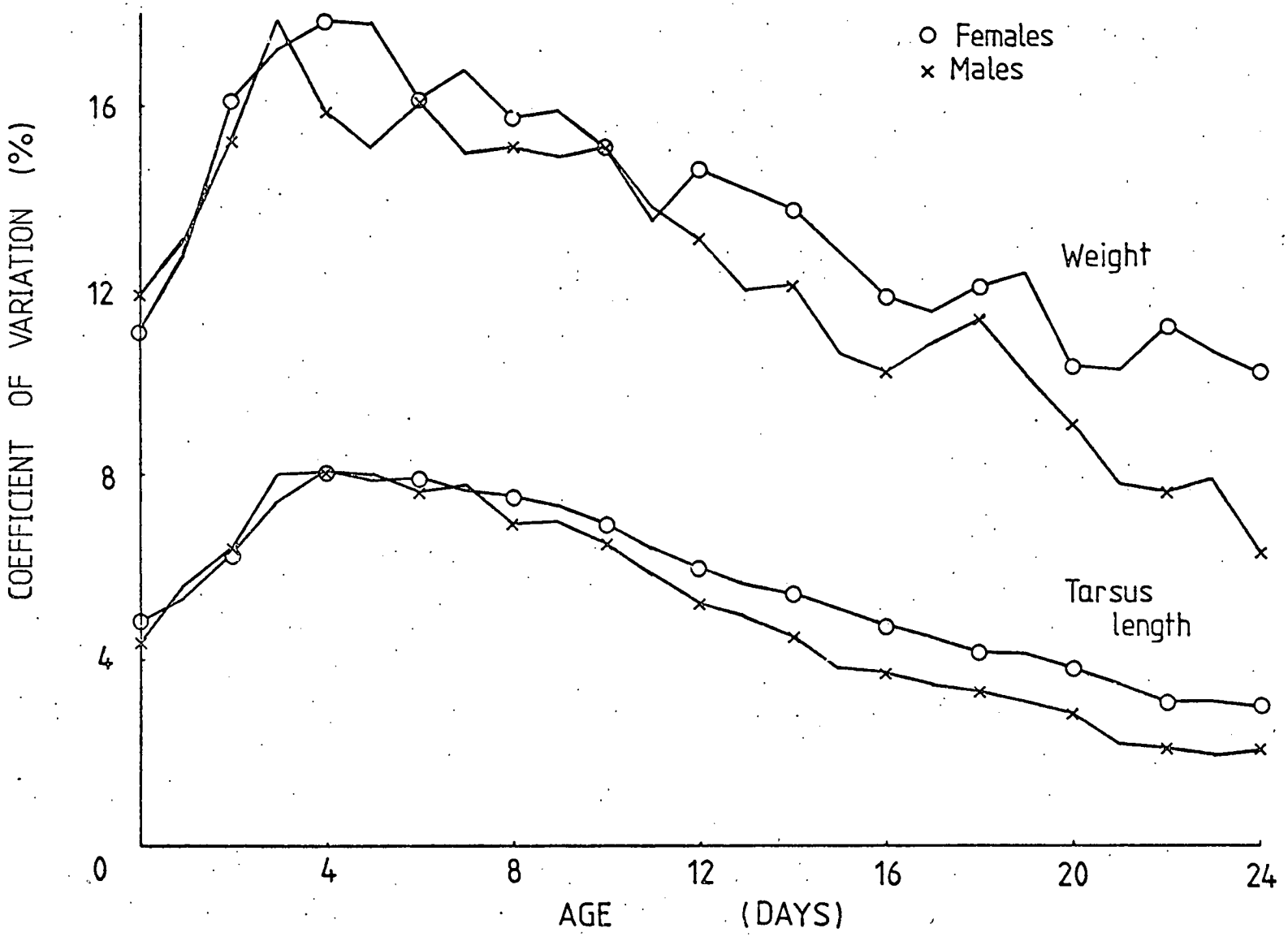


FIGURE 9 - COEFFICIENTS OF VARIATION (100 x standard deviation/mean) IN WEIGHT AND TARSUS LENGTHS OF EACH SEX

but that in later growth the birds which grew more slowly at first compensated so that the variation was reduced steadily. The decrease in variation was not biased by the deaths of those birds which could not make the compensatory growth (and were excluded from the calculations), because a decrease in variation was still noted when only Annan valley birds, of which very few died, were considered separately.

The variability of the growth of each individual was indicated by the standard errors of the growth rates calculated over the standard periods. For each of the three measurements and for both sexes, the standard error was significantly negatively correlated with the growth rate. These correlations indicated that the birds with high growth rates also grew evenly, while birds with low growth rates were more subject to fluctuations within their growth patterns. They were also more likely to die if these fluctuations became too severe.

2.6 Consideration of growth data

2.6.1 Variation within and between broods

The validity of the use of means of the growth rates (relative to the overall mean for each sex) for each brood was tested by analyses of variance, which showed that the variation in individual growth rates was significantly greater between broods than within broods for each measurement ($F_{51,139} = 9.58$, $P < .01$ for weight; $F_{51,139} = 5.06$, $P < .01$ for tarsus; $F_{48,132} = 7.51$, $P < .01$ for primary). It was thus justifiable to compare means of growth rates between broods. The significance held irrespective of brood size.

The within-brood variation in rate of weight-gain, which was the measurement with greatest variation within broods, was greater in broods with low rather than high mean growth rates. This was expressed as a linear relationship between the within-brood log mean squared deviation and the mean rate of weight gain for the brood ($r = -0.542$, 50 d.f., $P < .01$). This correlation showed that under good conditions when growth rates were high, all the nestlings in a brood fared equally well, while under poor conditions a much wider spread of growth rates resulted. This effect would have been even greater if data from the runts (excluded from this analysis) could have been used, since these were generally found in nests with poor mean growth rates. A similar increased spread in growth rates where overall growth was poor was noted in Snowy Owls by Watson (1957).

Rates of weight gain also varied more between broods than the other measurements, and the respective standard deviations over the total sample, with means of approximately 100 in each case, were 13.5 for weight, 6.3 for tarsus, and 8.1 for primary. The growth rates in the three different measurements were highly correlated with one

another. The correlation coefficients between mean rates for each brood were $r = 0.667$, 50 d.f., $P < .01$ for weight and tarsus; $r = 0.810$, 47 d.f., $P < .01$ for weight and primary; $r = 0.667$, 47 d.f., $P < .01$ for tarsus and primary.

2.6.2 Year

There were no significant differences between the three years of the study either in total or in Ae Forest and Annan valley sites considered separately, so the data from all three years could be used together when the other factors discussed here and in section 2.7 were considered.

2.6.3 Brood size

The brood size during the early part of the growth period was not significant in explaining differences in growth rates between nests in any of the areas taken separately or together for any of the measurements. The implication of this result was that, except in the remote and central forest areas, where the situation was complicated by high mortality (section 2.9), growth rates were the same amongst broods of five as amongst broods of three. This result might have arisen if large broods contained relatively many males (which were smaller than females) than small broods. However there was no difference in sex ratio between brood sizes within either major area. Neither could this result be explained by differences between areas, such that the large broods tended to be in areas with high growth rates, since there were no significant differences in brood size up to 11 days after hatching between the six areas, and no effects due to brood size within areas.

For growth rates to be independent of brood size, the adult birds must have provided proportionally more food for large than for small

broods. This could have been partly compensated by a lower food requirement per bird, since heat loss and hence energy requirement would have been lower in the larger brood, but this compensation would only have begun after the female ceased to brood the nestlings, at about 11 days old. No measurements were taken of heat loss from the broods, but any decrease in food requirement due to reduced heat loss in a larger brood would not have compensated during the first ten days for the extra food required to raise more nestlings. This result will be discussed further later (section 2.13.2).

2.6.4 Hatching order

For every brood for which any order in hatching could be determined within either or both sexes, the order in weight gain was also found. Males and females within each brood were compared separately for this purpose so as to exclude any possible bias in the result if females, which hatched earlier than males in Ae Forest (Table 5), consequently achieved higher growth rates. Each brood was classified according to the sign of the rank correlation coefficient between hatching order and weight gain order in each sex, and the broods were grouped by size and by area. In each case the binomial probability of at least the observed number of positive correlations was calculated, under a null hypothesis that positive and negative correlations were equally likely (Table 7).

Although the samples were small, significantly many positive correlations were observed in broods of four and five, but not in broods of three, and in total in both major areas. There was a highly significant number of positive correlations in the total sample ($P < .001$). The results for large broods may have been due to the greater spread of hatching in the broods of four and five (Figure 8), which allowed

TABLE 6 - MEAN HATCHING DATES[1] OF NATURALLY HATCHED BROODS IN DIFFERENT AREAS

Area	Number of broods	Mean hatch date ± standard error
Ae Forest, remote	5	20.8 ± 3.0
Ae Forest, central	8	22.4 ± 1.2
Ae Forest, edge	7	20.1 ± 2.4
St Ann's	13	14.5 ± 1.4
Templand	7	22.3 ± 3.0
Moffat	5	21.8 ± 1.8
Ae Forest, total	20	21.2 ± 1.2
Annan valley, total	20	17.2 ± 1.6

Significance of difference $t_{38} = 2.00$, $P < .1$

[1] Values given are dates taken from 1st June = 1. Hatching date is the date on which the first egg hatched.

TABLE 7 - TOTAL NUMBERS OF POSITIVE AND NEGATIVE RANK CORRELATION COEFFICIENTS BETWEEN HATCHING ORDER AND GROWTH RATE ORDER

Females and males taken separately within each brood, and results for either sex included here.

Category	Signs of r +	Signs of r -	Probability[1]
Broods of 3 (and 2)	5	2	0.227
Broods of 4	10	3	0.046
Broods of 5 (and 6)	12	0	<0.001
Ae Forest	12	1	0.002
Annan Valley	12	4	0.038
Total	27	5	<0.001

[1] One-tailed probability using the binomial distribution of a result at least as extreme under the null hypothesis that correlations of either sign were equally likely.

the earliest hatched birds to gain dominance in the nest and so attain the highest growth rates.

The mean rates of weight gain, expressed as percentages of the means for each sex, were compared directly according to hatching order within the whole brood, for each brood size and area (Table 8 and Figure 10). When two nestlings could not be separated into hatching ranks, the mean of their growth rates was taken for both ranks. The differences between broods were too great for differences due to hatching order to be significant. However the mean values reflected the decreasing trends with hatching order shown earlier, particularly in forest broods and valley broods of five.

2.6.5 Hatching date

Growth rates decreased as hatching became later. Correlations between hatching date and growth rates were $r = -.250$, 50 d.f., not significant, for weight; $r = -.146$, 50 d.f., not significant, for tarsus; and $r = -.297$, 47 d.f., $P < .05$, for primary growth. The result for primary growth showed an overall decrease in growth rate of 0.35% per day. When the data were split according to area, hatching date was uncorrelated with rates of weight gain in Ae Forest ($r = -.024$), but was significantly negatively correlated ($r = -.527$, 20 d.f., $P < .02$) with rate of weight gain in the Annan valley. This result indicated a decrease of 0.5% per day in rate of weight gain in the valley. It is difficult to understand this division, which suggested a deterioration in conditions during the breeding season in the area which was generally good for growth, but no change in the poor area. The same lack of correlation in Ae Forest held when broods introduced artificially from elsewhere were excluded from the regression.

TABLE 8 - MEAN RATE OF WEIGHT GAIN[1] OF NESTLINGS, DIVIDED ACCORDING TO HATCHING ORDER[2] AND BY BROOD SIZE AND AREA

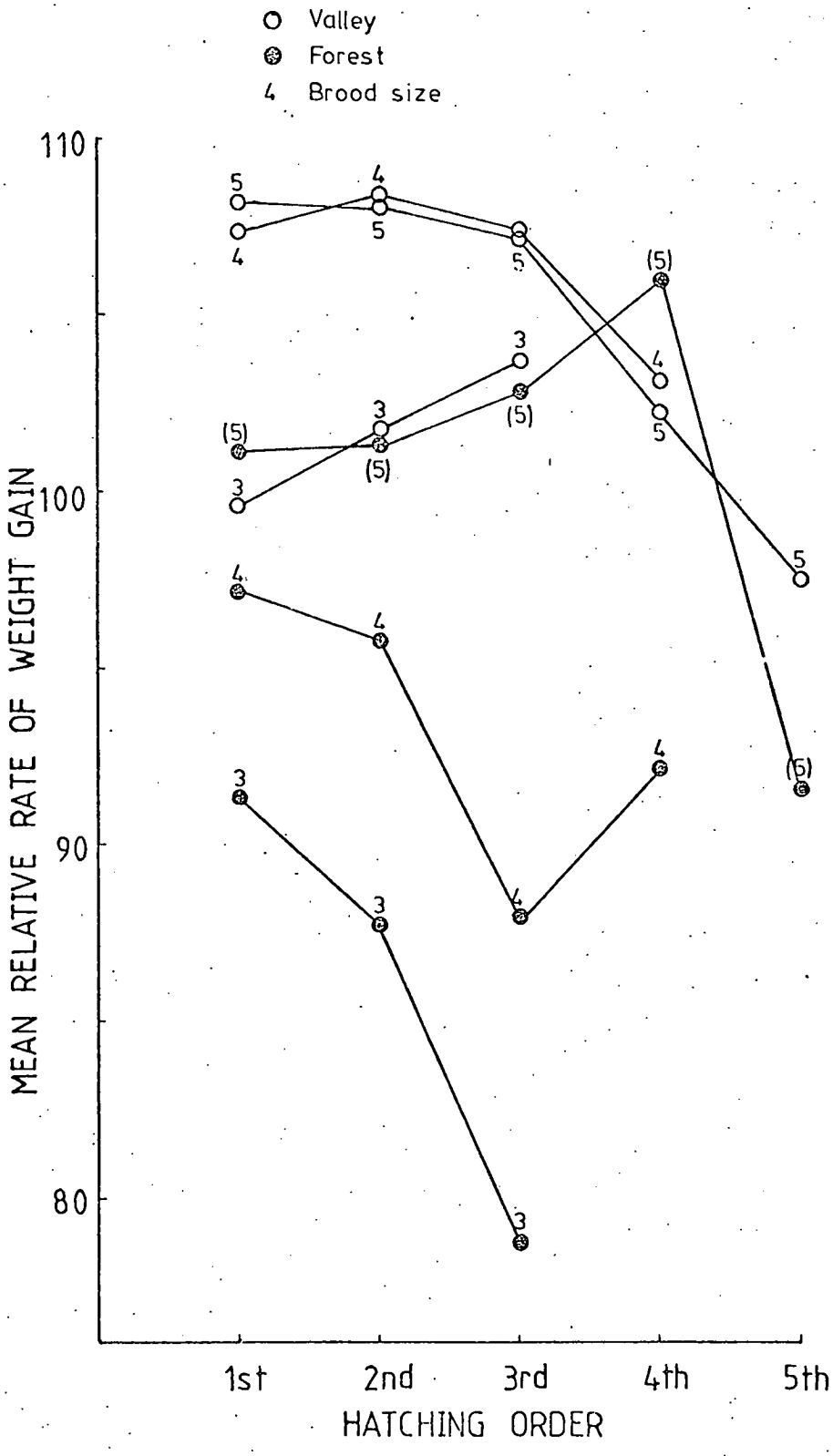
See Figure 10.

Area	Brood size	Number of broods	Hatching order				
			1st	2nd	3rd	4th	5th
Ae Forest	3	10	91.4 ± 7.6	87.8 ± 7.2	78.8 ± 6.9		
	4	8	97.4 ± 5.8	95.8 ± 6.5	88.0 ± 5.5	92.2 ± 6.7	
	5	3	101.2	101.2	102.9	106.0	91.6
Annan Valley	3	5	99.7 ± 3.3	101.8 ± 3.9	103.7 ± 2.7		
	4	8	107.4 ± 2.1	108.5 ± 2.3	107.4 ± 2.8	103.2 ± 6.4	
	5	6	108.2 ± 1.7	108.2 ± 1.7	107.3 ± 2.7	102.4 ± 3.0	97.6 ± 5.4

[1] Rate of weight gain expressed as a percentage of the overall mean for each sex.

[2] When hatching orders were tied, the mean growth rates of the tied birds were used.

FIGURE 10 - MEAN RATE OF WEIGHT GAIN[1] OF NESTLINGS, DIVIDED ACCORDING TO HATCHING ORDER, BROOD SIZE, AND AREA



[1] Relative to the overall mean for each sex.

The mean hatching date (Table 6) was significantly earlier in the St Ann's area of the Annan valley than in all the other sub-areas, where all the mean hatching dates were similar. The mean hatching date in the forest was four days later than in the valley, and although this difference was only significant at the 10% level, it confirmed that for earlier years found by Newton (1976).

2.6.6 Age of the adult female

The females breeding at every study nest were trapped, measured and ringed by I. Newton and M. Marquiss. They could be aged when they were first trapped as yearlings, two-year-olds, or older birds, so that their exact or minimum ages were known on subsequent recapture. The correlation between growth rate and the age of the female was not significant in any of the three cases (under 1% of the variation was explained). Since the male provides most of the food for the female and the brood, at least until about 14 days after hatching, his age might have been more relevant to the growth of the brood than that of the female. However only about 50% of the males at the study sites were trapped, and most of these were aged as adults, so that there were insufficient data with which to test the effect of the male's age on the growth rates of the brood.

2.6.7 Consistency between years of growth of broods reared by the same female or at the same site

The between-brood variation in rates of weight gain was analysed within the six sub-areas (whose importance will be described in the following section), in order to test for consistency in growth rates of broods raised by the same mother or at the same site in different years. The variation in growth rates between the five pairs of broods raised by the same female was slightly less than between broods in each area raised by different females ($F_{5,41} = 0.73$). Ten sites

were studied in two different years, and two sites in all three years. Growth rates varied as much between broods at the same site as between broods at different sites within each area ($F_{14,32} = 0.96$).

These two results, although not statistically significant, suggested that apart from the considerable variation between areas, some of the variation in growth rates was due to different females, but little was due to variation between nest sites within the areas. Again, as above, it might have been relevant to consider the adult males, rather than the females. However too few of the males were trapped, and none bred more than once at my study nests.

2.7 The relationship between growth rates and environmental factors

In order to find out whether growth rates were influenced by environmental factors, measurements for the nest sites relevant to the rearing of young were sought. In particular, since some of the adult birds were hunting at considerable distances from their nests (see later, section 4.3), the distance from the nest to the nearest source of abundant prey was thought likely to be important. Prey densities were known from the census work only for a few woods, but high densities were thought most likely to be found on good quality valley land. In a review of bird numbers in forests, von Haartman (1971) noted that soil productivity was an important factor. Total densities of birds in Finnish forests of equivalent types increased as the soil became richer. For this reason information on the land qualities in the study area was obtained from the Ordnance Survey Land Classification Map (1945). On this map land was classified according to its potential for producing crops. The classes given on the map which were found in the study area were:

3 - Good quality land, liable to flooding

4 - Good but heavy land

6 - Medium quality land

8 - Poor quality hill ground

Eleven environmental measurements were used in further regressions in which the growth rates were the dependent variables. These were:

(1) Area within 1 km of the nest which was shown as woodland on the 1-inch Ordnance Survey map (revised 1963), reduced by the areas windblown in 1968 and 1974. Measured in units of 4 ha.

(2) As (1), with a radius of 3 km from the nest and units of measurement 25 ha.

These two variables were chosen to test whether growth rates increased as the hunting area available within the ranges of 1 km and 3 km increased. (Sparrowhawks spent most of their time in woodland when hunting.)

(3) 'Ae': a simple variable given the value 1 for nests in the Ae Forest, and 0 for other nests (in smaller woods, mainly on lower ground).

(4) Altitude of the nest site above sea level, in feet.

(5) Distance of nest from the nearest farmyard (km): this was chosen as a measure of remoteness rather than under any assumption that farmyards were important sources of prey.

((6)-(11): Measurements taken from the land classification map.)

(6) Class of land at the nest site. When the site was near a boundary between two classes, the mean value was taken.

(7) Best land class within 1 km of the nest site.

(8) Best land class within 3 km of the nest site.

These two variables were chosen to test whether growth rate depended on the best land available within certain radii of the nest.

(9) Mean land class within 1 km of the nest site.

(10) Distance from the nest site to land of at least medium quality (class 6 or higher). This variable was zero when the site was on class 6 or higher class land.

(11) As (10), but taking good class land (class 4 or higher). These two variables were chosen to test whether growth rate depended on the distance from the nest to land of better quality.

Contrary to expectation, the growth rates were negatively correlated with the amounts of woodland around the nest (variables (1) and (2), Table 9A). It will be argued below that these were spurious results with no biological significance.

TABLE 9 - CORRELATION COEFFICIENTS BETWEEN MEAN GROWTH RATES AND ENVIRONMENTAL MEASUREMENTS, PARTICULARLY OF REMOTENESS OF NEST SITE FROM POSSIBLE PREY SOURCES.

For explanation of the variables, see Section 2.7.

(A) All nests, independent variables taken singly

Independent variable	Dependent variable: Weight	Tarsus	Primary
	N: 52	52	49
(1) Woodland within 1 km	-.459***	-.470***	-.505***
(2) Woodland within 3 km	-.475***	-.432**	-.567***
(3) 'Ae'	-.419**	-.489***	-.465**
(4) Altitude	-.426**	-.465***	-.408**
(5) Distance from farmyard	-.474***	-.454***	-.495***
(6) Land class at site	-.423**	-.421**	-.357*
(7) Best class within 1 km	-.399**	-.415**	-.387**
(8) Best class within 3 km	-.527***	-.547***	-.512***
(9) Mean class within 1 km	-.418**	-.452**	-.379**
(10) Distance to class 6 land	-.535***	-.331*	-.434**
(11) Distance to class 4 land	-.530***	-.529***	-.531***
% of variation explained by variables (3)-(11) together	43.16	34.90	30.70

(B) Regression coefficients, Ae Forest nests, weight gain only

N: 26

Distance to class 6 land	-3.08 ± 2.99
Distance to class 4 land	-5.15 ± 2.47
% explained	33.41**

Significance levels: * = 5%, ** = 1%, *** = 0.1%

Note: percentage of variation explained by a linear regression = $100r^2\%$, where r = correlation coefficient

Of the other variables, (8), (9), and (11) were most highly correlated with the growth rates (Table 9A). The correlation coefficients for each of the three dependent variables and each of the eleven independent variables were significant when each pair was taken singly. The multiple regressions on the nine variables (3)-(11) were also significant, and between 31% and 43% of the variation was explained. The remaining variation was due to random effects and to variables which could not be measured, of which the most important were probably the individual abilities of the parent birds in finding and capturing prey and in caring for the young.

These correlations showed that growth rates of nestlings decreased markedly with distances from good and medium quality land. A further regression, in which only data from the Ae Forest were taken, made it possible to divide the Ae nest sites into the three groups of approximately equal size mentioned earlier (p.16), according to their remoteness from land of the better classes. For these sites, variables (10) and (11) above were the best combination to explain variations in the rates of weight gain (Table 9B). A remoteness score was calculated for each site using the two regression coefficients, and the remote, central, and edge sub-areas were delimited by two arbitrarily assigned scores, such that approximately equal numbers of sites fell in each sub-area. Each area was represented by at least two nests in each of the three years of the study (Table 1).

Variables (1) and (2) were rejected by comparison with the other variables, because the amount of woodland around the nest was highly correlated with the remoteness of the site, and the type of wood varied from dense plantation to mature mixed woodland. The remote forest nests were completely surrounded by woodland; the forest edge nests half surrounded; and the nests in the valley had little

woodland within the set radii. The correlations found between growth rates and variables (1) and (2) were thus spurious consequences of the occurrence of large areas of the poorest woodland in the most remote areas. Ae Forest and Annan valley data taken separately showed further the dependence between the amounts of woodland and remoteness. In Ae Forest, the rate of weight gain and the amount of woodland within 1 km were negatively correlated, but the relationship did not hold when the 3 km radius was taken. This was because there were areas of moorland within 3 km of the remote sites, while sites in the centre of the forest were surrounded by woodland for over 3 km radius. Thus it was the remoteness and not the amount of woodland which was important in influencing growth rates. At the valley sites growth rates were unrelated to the (much smaller, but variable) amounts of woodland within 1 km and 3 km.

Since the Sparrowhawk obtains most of its prey in woodland and at woodland edges, it might have been possible that prey availability, and hence growth rates, were correlated positively with the amount of woodland within a certain radius of the nest. However negative correlations, such as those found, could not be explained biologically. Some of the Annan valley sites had as little as 5% woodland cover within 1 km and 3 km of the nest, yet the nestlings achieved high growth rates, so the amount of good woodland required for the successful raising of a brood was very little. Other cover, such as tall hedges or clumps of trees, was sometimes available, but was of limited area and might not have been shown on the map (and thus was not included in the data analysed). However such cover could have been important to Sparrowhawks as hunting sites.

In sparsely wooded areas, Sparrowhawks are possibly prevented from breeding only through a lack of suitable nest sites, not through a lack of feeding areas or of food.

Growth rates based on the mean values of the measurements in each of the sub-areas and also in the whole Ae Forest and the Annan valley were calculated (Table 10 and Figure 11). The significant differences between the forest sub-areas and between the Ae Forest and Annan valley areas confirmed the earlier results, which showed growth rates inversely related to distance from good quality land. The growth rates attained by nestlings on the edge of the forest were almost as high as those in the valley.

It should be noted that the distances from good and medium quality land were used only as objective measurements of remoteness of the different sites, without any implication that these were the areas used by the adult birds to obtain prey. Neither was it claimed that land quality could be used to predict habitat quality for Sparrowhawks. As it happened, the growth rates observed were correlated with the distances from certain types of land to a greater extent than with any other measures of remoteness. These relationships will be discussed with reference to song-bird census data in Chapter 4.

TABLE 10 - GROWTH RATES CALCULATED FROM THE MEAN MEASUREMENTS OF NESTLINGS IN SIX DIFFERENT AREAS.

The values given are the regression coefficients in g. or mm. per day, with their standard errors.

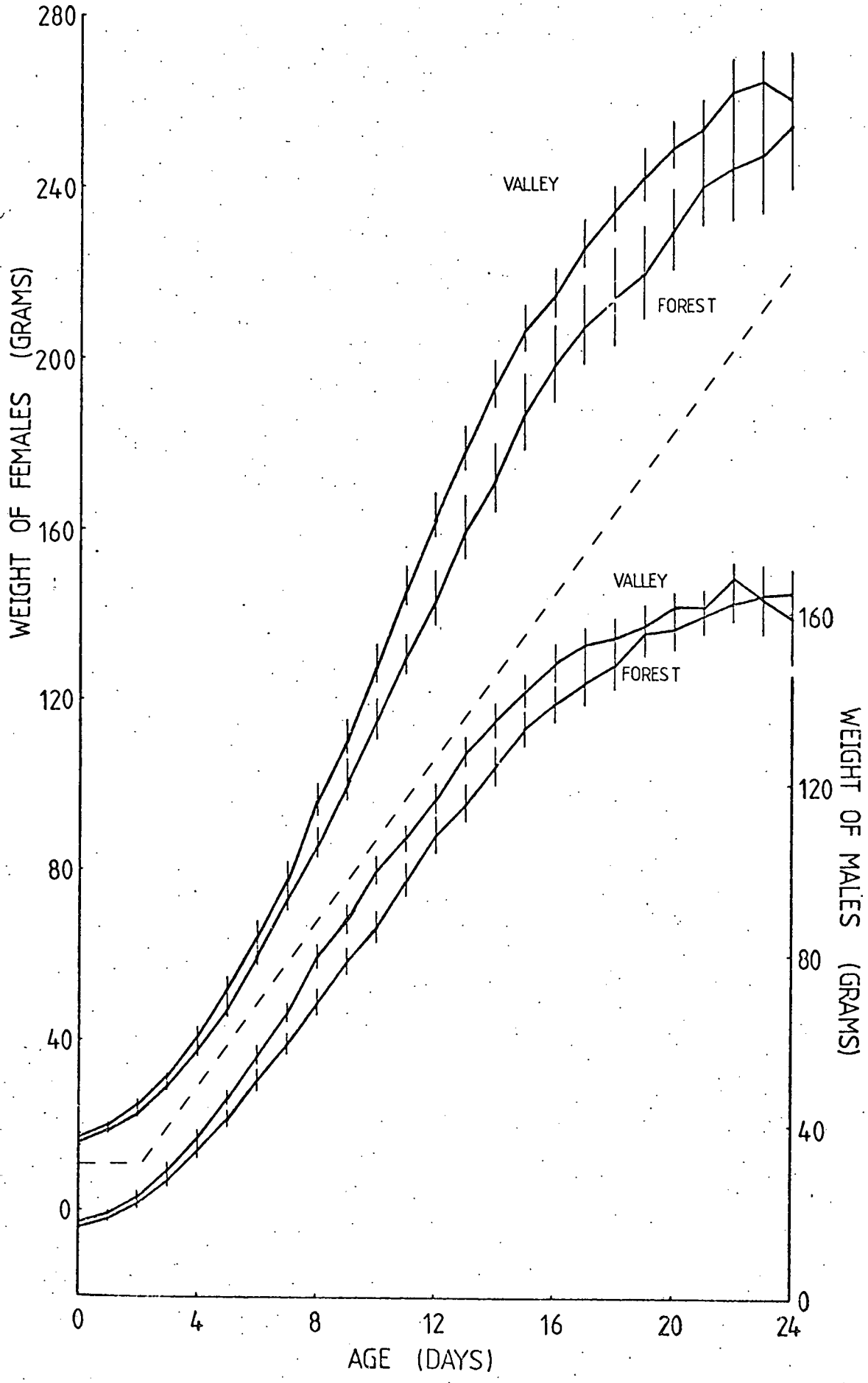
Males

Area	Number of nestlings	Weight	Tarsus	Primary
Ae Forest, remote	10	7.77 ± 0.13	2.94 ± 0.06	3.48 ± 0.05
Ae Forest, central	20	9.16 ± 0.10	2.96 ± 0.03	3.57 ± 0.05
Ae Forest, edge	20	9.80 ± 0.14	3.06 ± 0.03	3.65 ± 0.03
St Ann's	17	10.04 ± 0.20	3.22 ± 0.03	3.79 ± 0.03
Templand	11	9.88 ± 0.11	3.23 ± 0.04	3.78 ± 0.03
Moffat	9	9.73 ± 0.11	3.09 ± 0.03	3.54 ± 0.03
Forest of Ae total	50	9.22 ± 0.10	2.99 ± 0.03	3.60 ± 0.02
Annan valley total	28	9.98 ± 0.15	3.23 ± 0.03	3.79 ± 0.03
Significance of difference		P < .001	P < .001	P < .001

Females

Area	Number of nestlings	Weight	Tarsus	Primary
Ae Forest, remote	11	11.47 ± 0.46	3.23 ± 0.06	3.72 ± 0.08
Ae Forest, central	19	14.66 ± 0.12	3.38 ± 0.03	3.94 ± 0.06
Ae Forest, edge	13	15.59 ± 0.32	3.29 ± 0.03	4.11 ± 0.05
St Ann's	29	16.75 ± 0.16	3.50 ± 0.04	4.35 ± 0.04
Templand	25	15.53 ± 0.29	3.48 ± 0.03	4.15 ± 0.03
Moffat	7	14.16 ± 0.33	3.28 ± 0.04	4.12 ± 0.08
Forest of Ae total	43	14.18 ± 0.12	3.32 ± 0.03	3.95 ± 0.05
Annan valley total	54	16.19 ± 0.19	3.49 ± 0.04	4.26 ± 0.03
Significance of difference		P < .001	P < .001	P < .001

FIGURE 11 - MEAN WEIGHTS OF NESTLINGS IN AE FOREST AND THE ANNAN VALLEY



2.8 The effect of wet weather on growth

Records of the weather, including the duration of rainfall during the daylight hours, were kept in the three seasons, so that it was possible to test whether the growth of nestlings was reduced in wet weather. Mortality will be considered in the following section.

In each year there were five or six days during the main nestling period (15 June - 15 July) on which rain fell for more than four hours. For each (calendar) day the mean weight, tarsus and primary length increases of the individual nestlings were calculated over the total sample, and these were compared with the increases in the mean measurements for a set of nestlings with identical ages. The actual increases were expressed as percentages of the increases in the means. Only the main growth periods were taken: 4-18 days for weight; 2-15 days for tarsus; 8-20 days for primary.

The most important factor which affected the relative growth of the nestlings was the interval between measurements, which could not practicably be maintained at 24 hours. The mean time difference between the measurements on each successive day over all the nest visits was calculated, and a standard day-length of 17 hours possible feeding time was added to calculate the number of daylight hours between visits. The number of hours of rainfall in the day was used as an independent variable together with the mean time between visits in multiple regressions in which the increases in weight, tarsus, and primary relative to the means for appropriate ages were the dependent variables (Table 11). Since the nests were spread over a wide geographical and altitudinal range, the duration of rainfall varied considerably between nests in the Annan valley and those in the higher parts of the Ae Forest. Data from the lower Ae Forest were used here to give an average measure of the daily duration of rainfall.

The regression on the variable "time", the mean daylight hours between visits, was highly significant for all three measurements in 1973 and 1974, and for the three years taken together, but was not significant in 1975. Since growth is a continuous process, a highly significant correlation between daily growth and the time interval was expected. The variation in the time variable itself decreased as my routine became more standardised, from a standard deviation of 3.2 hours in 1973 to 1.9 hours in 1974 and 0.9 hours in 1975. The amount of variation in the dependent variables explained by time decreased from year to year as a result, so that the lack of significance in 1975 was due to the low variation in the time between visits.

The regression on the variable "rain", the number of hours of rainfall in the day, was significant for weight in 1973 (Figure 12) and 1974, when time had been taken into account, but was not significant for either of the other measurements in those years, or for any measurement in 1975. When the rainfall on the previous day was used instead of the rainfall on the day of the measurements, it gave significant regressions in 1975 for weight and primary (Table 11), but was not significant for any measurement in either of the other years. It was not possible to separate the rainfall data more accurately and use the actual number of hours of rainfall between visits, since both visits and rainfall were spread in time throughout the day.

Thus in each year there was a relation between relative weight gain and the duration of rainfall (Figure 12), although in one year the effect was delayed by one day, which was probably an artifact of the method of measuring rainfall duration. For primary there was only one significant result, and for tarsus there was none. The variability of the relative weight increases was considerably higher than those of the tarsus and primary increases: the respective

TABLE 11 - THE EFFECT OF RAINFALL ON GROWTH. MULTIPLE REGRESSION COEFFICIENTS AND THEIR STANDARD ERRORS.

The dependent variables are relative increases between consecutive days (see text).

Year	Indep. variable	Weight	Tarsus	Primary
1973	Time[1]	13.3 ± 1.4***	4.1 ± 0.7***	5.9 ± 0.8***
	Rain[2]	-4.3 ± 1.9*	-1.2 ± 0.9	-1.1 ± 0.9
	% of variation expl.	80.6	64.0	75.0
	Sample size	26	26	23
1974	Time	12.0 ± 2.8***	4.1 ± 1.1**	6.0 ± 1.1***
	Rain	-6.7 ± 1.9**	0.8 ± 0.8	-0.5 ± 0.6
	% explained	56.2	43.2	63.1
	Sample size	24	23	22
1975	Time	10.5 ± 9.6	2.4 ± 1.3	1.0 ± 2.2
	Rain	2.5 ± 2.9	0.0 ± 0.7	-0.7 ± 0.7
	% explained	10.5	14.3	6.1
	Sample size	27	24	23
ALL	Time	12.7 ± 1.7***	3.8 ± 0.5***	5.6 ± 0.6***
	Rain	-2.3 ± 1.4	-0.1 ± 0.5	-0.7 ± 0.4
	% explained	43.9	47.2	58.9
	Sample size	77	73	68
1975	Time	18.8 ± 8.5*	2.9 ± 1.3*	0.6 ± 1.9
	Rain on previous day	-7.8 ± 3.1*	0.9 ± 0.7	-2.3 ± 0.8**
	% explained	27.3	29.9	28.6
	Sample size	27	23	23

Significance levels of the coefficients: * = 5%, ** = 1%, *** = 0.1%

[1] Time = number of hours of daylight between visits on consecutive days.

[2] Rain = number of hours of rainfall on the day concerned.

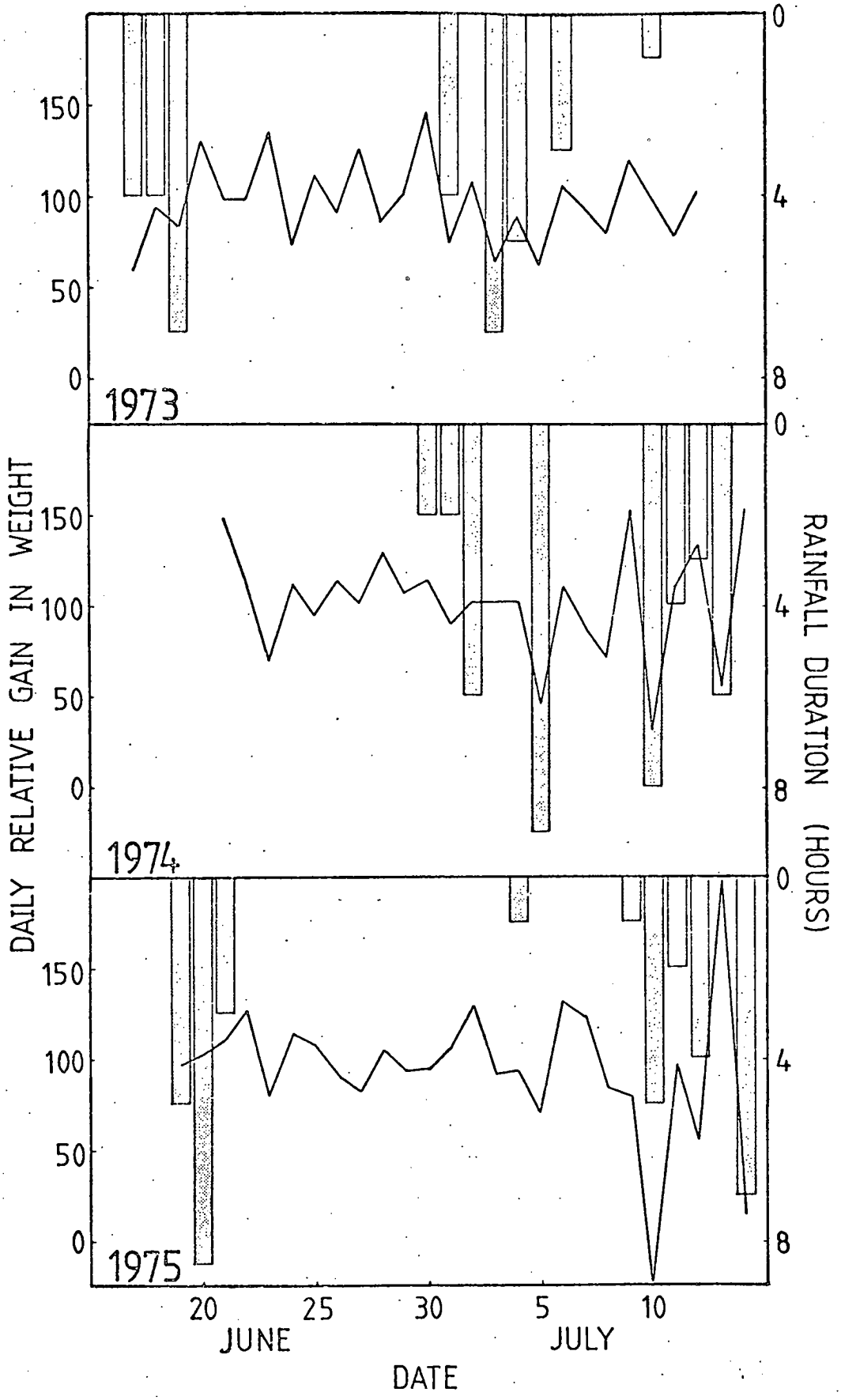


FIGURE 12 - THE EFFECT OF RAINFALL ON WEIGHT GAIN[1]

[1] In 1975 the rainfall on the day previous to the weight measurements is shown

overall standard deviations not explained by the time variable were 32.0, 9.0, 9.0, with means approximately 100 in each case.

These results showed that the processes of bone and feather growth were regulated so that they varied little from day to day, and were less affected by variations in the food supply, such as those caused by wet weather. Weight increases were by contrast much more variable, so that the rate of increase was reduced in periods of wet weather when the food intake would have been lowered.

These results confirm those of Mulliner & Reeves (1974) and Moss M. (1975), who found during their studies of three Ae Forest nests in two years that the nestlings were fed significantly less often during periods of rain than in dry weather, presumably because hunting ability was impaired in rain.

The growth strategy of the nestlings was to maintain the essential bone and feather growth, and to make this possible they were able to tolerate relatively large drops in rate of weight gain. In the nestlings which died, tarsus and primaries did not stop growing until weight had decreased for one or two days. Similar results have been found for other birds; for example feather growth in Robins was unaffected when weight fluctuated (Lack & Silva 1949), and Manx Shearwaters maintained their feather growth through periods of starvation (Harris 1966). Weight gain in House Martins was much more variable than the feather growth rate early in the nestling period, although they were equally variable later (Bryant 1972). However feather growth in Swifts was severely retarded in bad weather (Lack & Lack 1951).

2.9 Mortality of nestlings

46 (21%) of the nestlings which survived 2 days from hatching died before they were 24 days old (see footnote, p.20). A further 6 died within 2 days of hatching,but the causes of death were unknown, and the information available on these birds was so limited that they were not considered further. The survival rates from 2 days in Ae Forest (67%), and in the Annan valley (94%), were significantly different ($P<.001$). Within the forest, the edge area and the other areas also differed significantly with 97% and 52% of nestlings being fledged respectively ($P<.001$), (Table 12). The same two pairs of areas also differed highly significantly in the mean number of young fledged per brood, and the percentage of nests in which all the young were fledged ($P<.01$ in every case), (Table 12). There were no differences between the forest edge area and the Annan valley areas. The Moffat area fledging rate (75%) was intermediate, but included one nest where all four nestlings slowly starved for no apparent reason.

Several causes of mortality in nestlings could be identified (Table 12). The most frequent was starvation, through competition with other nestlings, and this accounted for 15 birds (7% of the total number of nestlings). Death was preceded by several days of poor growth, often from hatching, and eventual weight loss in several cases. Starvation was most frequent in the remote forest nests, where at least one nestling starved in 5 of the 7 nests. 8 of the 15 died when aged 12-16 days, and in three broods, two young starved; the first at 12-13 days, and the second at 18 days. A significantly large number, 9 of the nestlings in the 12 broods concerned, were the last to hatch, and in several of these cases, these birds competed poorly with their siblings before eventually dying. Two of these

TABLE 12 - MORTALITY OF NESTLINGS BETWEEN 2 AND 24 DAYS OLD IN EACH AREA, AND CAUSES OF MORTALITY.

	Remote	Central	Edge	St Ann's	Templand	Moffat	Ae Forest	Annan valley	Total
Number of nests	7	11	9	13	9	5	27	22	54
Number of young at two days	28	43	35	50	38	21	106	88	215
Young per nest at two days	4.00	3.91	3.89	3.85	4.22	4.20	3.93	4.00	3.98
Number of young at 24 days	14	23	34	46	37	15	71	83	169
Young per nest at 24 days	2.00	2.09	3.78	3.54	4.11	3.00	2.63	3.77	3.17
% of young fledged	50	53	97	94	97	75	67	94	79
% of nests that were wholly successful[1]	0	37	89	85	89	60	44	86	63
Causes of mortality: number of nestlings dying from:									
Starvation/competition	7	3	1	3	1		11	4	15
Wet weather	4	6				1	10		11
Predation[2]		7					7		7
Desertion by female	3	3					6		6
Dragged from nest by female				1		1		1	2
Unknown cause		1				4	1		5

[1] i.e. all nestlings fledged. Two nests where nestlings were dragged from the nest by the female were counted as successful.

[2] Two nestlings found alive at the foot of the nest tree were counted as predated.

runts hatched two days later than the remainder of the brood, and one of them, at a nest in the St Ann's area where the other nestlings grew well, hatched three days after its siblings and died after 6 days. 6 of the 7 nestlings to starve which were sexed were males, but although this suggested differential mortality between the sexes, it was possible that females died at an earlier stage, and so formed the majority of the 8 unsexed nestlings which starved. The remains of the nestlings were usually eaten by the other members of the brood or by the adult female.

To summarise, starvation occurred most frequently where the food supply was poorest, and was most likely in the youngest nestling of the brood.

11 nestlings (5%) from 5 broods died in two periods of prolonged rain on 14-15 July 1974 and 14-15 July 1975. All the nestlings concerned were aged 18-23 days, when their developing feathers gave them little protection from water, while their down became sodden, leading to death after several hours. Two complete broods of three and four died, probably without receiving any protection from the adult hen. The other deaths were of two nestlings in a brood of five, and in two cases the smallest nestling of a brood of four. These birds were probably unable to obtain shelter with their siblings under the wings of the adult hen, for lack of space. Although these four nestlings had all shown relatively low growth rates, they would probably have survived if the weather had remained dry. Wet weather deaths occurred equally in nests in Norway Spruce and in the more exposed larch, and all except one were in the remote or central forest areas (Table 12).

A further 7 deaths (3%), from three broods, were attributed to predation by Tawny Owls. In all three cases involved, Tawny Owl

feathers were found close to the nest, suggesting that there had been a struggle. Two broods of three were affected in 1973 in the central forest area, when one brood disappeared completely aged 12-14 days, and in the second, one nestling was found dead 16 days after hatching, and the other two young were still alive near the foot of the nest tree. These two nestlings were transferred to other nests, but have been included in the mortality figures since they would have died without our intervention. The remaining death was in 1974 at a nest site adjacent to those which suffered predation in 1973. The youngest of a brood of four, aged six days, was found dead below the nest.

Two broods of three nestlings, one in the central and one in the remote forest area, were deserted by the female when they were 11 days old. Their weights dropped sharply, by up to one-third, before they died two days after desertion. In neither case was prey left on the nest by the male in the female's absence, so her desertion might have followed the male's death or desertion.

During the first week after hatching, the adult hen would brood the nestlings almost continuously, and when flushed she was liable accidentally to drag a nestling out from the nest. Precautions were taken to prevent this, by approaching the nest without stealth, so that the hen would be warned of the impending disturbance, and leave carefully. However on a few occasions a small nestling was dragged from the nest and fell to the ground, resulting in two deaths. These were excluded from the calculations of mortality rates (Table 12) because they were due solely to my interference.

The difference in mortality rates between Ae Forest and Annan valley was also found in 1971-3 by Newton (1976), working in the same areas. He excluded mortality due to desertion, predation or accident,

and found 4% mortality (5% in this study) in the Annan valley, and 13% (20% this study) in Ae Forest. Thus mortality was slightly lower in 1971-3 than in 1973-5.

Mortality was considered in relation to brood size at two days (Table 13). Only mortality due to starvation or wet weather was included, because I thought that other causes were likely to be independent of brood size. The remote and central Ae Forest sub-areas were separated from the remainder of the study area, and in these sub-areas mortality reduced most of the broods of more than three nestlings to broods of three (apart from the two broods reduced to zero in prolonged rain). The different initial brood sizes resulted in broods whose mean sizes did not differ significantly at fledging. By contrast, in the remaining areas all the mortality occurred in broods of four, and the mean numbers of nestlings fledged increased with the initial brood size (Table 13).

TABLE 13 - MORTALITY[1] IN RELATION TO BROOD SIZE TWO DAYS AFTER HATCHING.

Brood size	Ae Forest, remote and central areas			Other areas		
	No. of broods	% young fledged	No. fledged per brood	No. of broods	% young fledged	No. fledged per brood
3	2	100	3.0	8	100	3.0
4	9	64	2.6	18	92	3.7
5	2	50	2.5	8	100	5.0
6	1	50	3.0			

[1] Due only to starvation or wet weather. Broods deserted or predated were excluded.

2.10 Sex ratio of nestlings

Sex ratios were compared between the different areas when the nestlings were two days old (young were sexed retrospectively), and at fledging (Table 14). The replacement clutches and nestlings transferred between nests were excluded, so that only nestlings hatched naturally in each area were counted. In the few cases where eggs or nestlings were moved from nests within the study, they were counted as if they had hatched in the original nests.

There was an excess of males in Ae Forest, and a marked excess of females in the Annan valley (Table 14). The differences between the two major areas were significant ($P < .02$) both at two days and at fledging. This trend was in the same direction, to varying extents, in all three years. There was very little difference in sex ratio between two days and fledging, showing no differential mortality of the sexes.

The low proportion of males in the valley might have been due to several broods which consisted of either four or five females, or four females and one male. In case the bias towards females arose within broods, the numbers of broods with excesses of males and of females at two days were counted in the two areas (Table 15). Again the difference between the two areas was significant ($P < .02$), and the probability of a result as extreme as that observed in the valley was .022.

I cannot explain the real difference observed in sex ratio in the two adjacent areas, between which exchange of individuals has been recorded several times. If all seven nestlings that died unsexed in the forest were females, and all four in the valley were males, the respective sex ratios at hatching would have been 103 and 63 males to 100 females respectively. This difference would no longer have been statistically significant, but this situation would have been highly unlikely.

TABLE 14 - SEX RATIOS OF NESTLING SPARROWHAWKS AT 2 DAYS OLD AND AT FLEDGING (24 DAYS OLD) IN EACH AREA.

Only natural hatchings are included; eggs and nestlings transferred between nests counted only at nest of origin. Sex ratio = number of males to 100 females.

	At two days				At fledging		
	Males	Females	Unknown	Sex Ratio	Males	Females	Sex Ratio
Ae Forest, remote	9	8	1	113	5	6	83
Ae Forest, central	16	11	1	145	11	6	183
Ae Forest, edge	11	9	0	122	11	9	122
St Ann's	19	29	2	66	17	29	59
Templand	8	20	0	40	7	20	35
Moffat	7	6	6	117	7	6	117
Ae Forest, total	36	28	2	129	27	21	129
Annan valley, total	27	49	2	55	24	49	49
Significance of difference		$\chi^2_1 = 6.03$ $P < .02$				$\chi^2_1 = 5.70$ $P < .02$	

TABLE 15 - NUMBERS OF NATURALLY HATCHED BROODS WITH A PREDOMINANCE AT TWO DAYS OLD OF EITHER SEX IN THE TWO MAJOR AREAS.

Area	Broods with an excess of: Males	Females	Two-tailed binomial probability
Forest of Ae	8	5	.582
Annan valley	3	13	.022
Difference between the areas $\chi^2_1 = 5.58$, $P < .02$			

2.11 Attendance at nest and behaviour of adult females

On every nest visit a note was made of whether the adult female was on the nest, heard or seen in the vicinity, or undetected. As mentioned earlier, in 1975 behaviour was further classified subjectively into "agitated", with calls repeated frequently throughout the visit, or "not agitated", with only occasional calls. Most adult females did not leave the nest until I could see it, so that their presence could always be detected, but less than 10% of them habitually left well in advance of disturbance, and so I detected them seldom even when the nestlings were small.

The percentage of visits on which the hen was detected was calculated in relation to the age of the oldest nestling for the Ae Forest and Annan valley nests, and to smooth the day-to-day fluctuations, four-day running means were plotted (Figure 13).

Until the nestlings were eleven days old, they were brooded by the female for most of the time, and the attendance score fell gradually from 90% to 77%, with little difference between the areas. Over the remaining period, from 11 to 24 days, the females started hunting, and the attendance scores fell further, to 32% in the forest, but only to 66% in the valley. The considerable difference between the two areas developed from day 11 (Figure 13). For each nest where observations continued at least to 20 days from hatching, the percentage attendance of the female was calculated from day 11 onwards. When attendance scores for nests in each area were combined (Table 16), the percentage was significantly higher in the Annan valley than in the Ae Forest, ($t = 3.74$, 43 d.f., $P < .001$), but differences between the forest areas were slight.

In view of this observation, the attendance at each nest from day 11 was compared with the environmental variables of the nest site

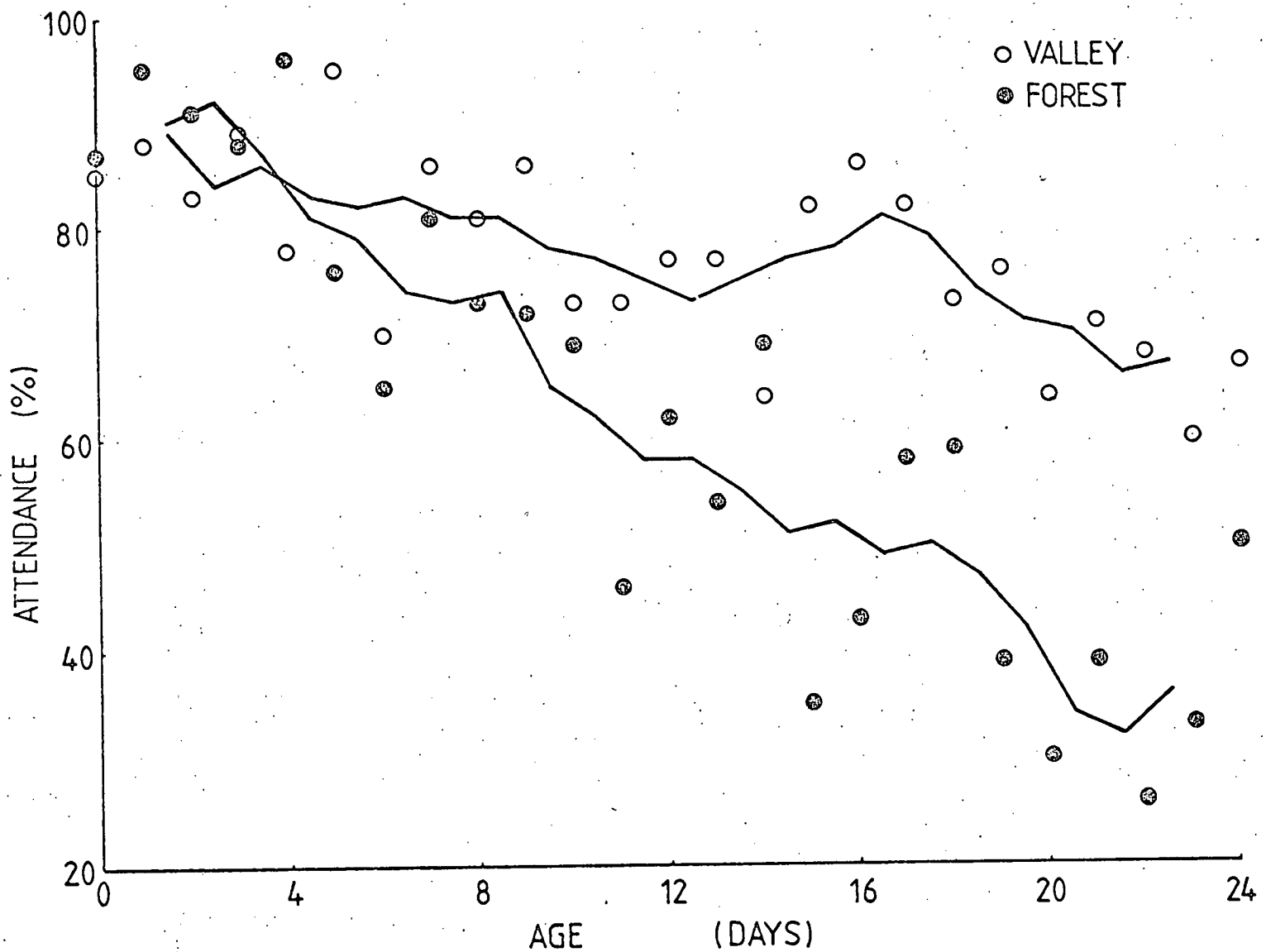


FIGURE 13 - THE PERCENTAGE OF VISITS TO NESTS IN EACH AREA ON WHICH THE ADULT FEMALE WAS DETECTED. The percentages for each age are plotted, and the joined lines show four-day running means.

TABLE 16 - PERCENTAGE OF VISITS TO NESTS IN EACH AREA FROM DAY 11 TO DAY 24 ON WHICH THE ADULT FEMALE WAS DETECTED.

Area	Number of nests	Number of visits	% attendance ± s.e.
Ae Forest, remote	6	79	47 ± 11
Ae Forest, central	8	102	42 ± 4
Ae Forest, edge	9	125	53 ± 9
St Ann's	13	166	76 ± 7
Templand	9	114	68 ± 7
Moffat	5	63	51 ± 13
Ae Forest, total	23	306	48 ± 5
Annan valley	22	280	73 ± 5
Significance of difference			P<.001

TABLE 17 - CORRELATIONS[1] BETWEEN PERCENTAGE ATTENDANCE OF FEMALE AT NEST ON DAYS 11-24 AND ENVIRONMENTAL MEASUREMENTS AT NEST SITE (see section 2.7).

Variable	Correlation
'Ae'	-.459**
Altitude	-.347**
Distance from a farmyard	-.396**
Land class at site	-.377**
Best land class within 1 km	-.364**
Best land class within 3 km	-.459**
Mean class within 1 km	-.428**
Distance to class 6 land	-.242
Distance to class 4 land	-.484**

[1] Correlations with 46 degrees of freedom.

Significance levels: * = 5%, ** = 1%

location described earlier (section 2.7). Attendance was significantly negatively correlated with each of the variables except the distance of the nest from medium quality land (Table 17), and the distance from the nest to good quality land explained the greatest amount of variation. Attendance was unrelated to brood size or the age of the female. The rates of weight gain and of tarsus and primary growth were correlated significantly with attendance ($P<.01$). The correlations suggested that low growth rates and infrequent attendance of the female were linked, although the relation may not have been a causative one since both were correlated with the same environmental factors.

The explanation for the high attendance where conditions for raising the young were good was that there the males could provide most of the prey required for the broods, possibly supplemented by the females hunting near the nest. By contrast, in poor areas, the females also had to hunt for much of the time, usually away from the nest area, so they would be detected less frequently than the females nesting in good areas. The females would start to hunt when the young no longer required brooding, when about 11 days old. Mulliner & Reeves (1974) noted abrupt decreases in the proportion of time which the female spent brooding when the nestlings were 10 and 11 days old respectively at the two nests studied. Their result matched the decrease in attendance found at day 11 here (Figure 13).

The more detailed observations of behaviour of females in 1975 showed that a total of 16 birds detected more than ten times were classified as agitated on 31% of all detections. The percentages for individual birds ranged widely, from two of 0% and one of 5% to one of 70% and one of 100%, showing that some individuals tended to have consistent behaviour patterns, which varied considerably between birds. The frequency of agitation was only slightly higher in the

forest than the valley, and further evidence that tenacity was an individual characteristic of the birds' behaviour was that its rate did not change during the nestling period. Birds most often observed were also the most agitated: the frequency of agitation and percentage attendance after day 11 were significantly correlated (Spearman rank correlation coefficient = 0.626, N = 16, $P < .01$). This might have been partly because birds which were least agitated might frequently have been present in the nest area but not remained undetected during the nest visits, on account of their silent habits. A further four females observed less than ten times each were recorded as agitated only once between them.

2.12 Survival of nestlings after fledging, from ringing returns

25 (15%) of the 169 nestlings to fledge had been recaptured or found dead by 31 December 1975. Only seven of these were known to have survived to their second calendar year of life. These numbers are small, and are likely to be increased in the future by the trapping of breeding birds which had not entered the breeding population by 1975, and by the chance recovery of ringed birds elsewhere. The sample is biased towards birds which were raised in Ae Forest, because several were trapped there in early autumn, when no trapping was done in the Annan valley.

Analyses of rankings of the rates of weight gain of the 15 males and 10 females known to have survived to independence among the total samples were made separately for each sex. In both cases the ranks of the birds subsequently recaptured or found dead did not differ from those expected from random samples of the same sizes (Mann-Whitney U test). To counter the bias towards the Ae Forest birds, the analyses were restricted to forest birds (13 males and 4 females), where the results again differed little from random samples, thus, chance of recovery was not related to growth rates.

It is difficult to draw any conclusion from these results, for several reasons. Several years will be required before all the 1973-5 nestlings have died, and until recaptures and recoveries are complete. The dispersive movements of the young birds after reaching independence are little known, although it is apparent even from the data available here that females disperse further than males: six of the seven birds recovered more than 20 km from the nest site were females, while all eleven trapped in the Ae Forest in autumn were males. However this may have been due to a habitat difference between the sexes; trapping was confined to forest areas. There is

insufficient evidence to determine whether there is any differential dispersion between birds of the same sex according to the quality of the nest territory where they were raised, or to their subsequent body condition.

2.13 Discussion

2.13.1 Sexual dimorphism

The extreme sexual dimorphism exhibited by the European and North American species of the genus Accipiter was discussed by Storer (1966) and Reynolds (1972), who showed how their dimorphism allowed the two sexes to specialise on prey of different size ranges, while any one pair of species was also completely separated by size. The same was true of Accipiters in West Africa (Brosset 1973), where the four species were divided as a result of sexual dimorphism into eight size classes with little overlap. None of these authors studied the development of dimorphism at the nestling stage.

In one of the few detailed growth studies that has been made on raptorial birds, Scharf & Balfour (1971) mentioned that adult female Hen Harriers were 50% heavier than adult males, but the authors did not separate the sexes in their presentation of nestling weight data. Possibly sex differences in weight developed much less rapidly than in the Sparrowhawk.

The present study showed that in one area eggs that gave rise to females had slightly shorter incubation periods than those producing males; that the weights of females diverged from those of males from the age of one day, although they were the same on the day of hatching; but that the other development of females was two or more days behind that of males. Related studies (Mulliner & Reeves 1974, Moss M. 1975) showed that female and male nestlings received equal amounts of food. Thus while the emphasis in females was on higher rates of weight gain in achieving the larger size, in males it was on faster development. This more rapid acquisition of skills may have enabled the males to compete equally for food with the much larger females in the brood, both while still in the nest and in the post-fledging period. The

growth strategies of the two sexes were thus complementary, and ensured that neither had a lower chance of survival in competition with the other.

2.13.2 Brood size

Lack (1954, 1966) suggested that the clutch size of most birds has evolved to correspond with the largest number of young which on average the parents can raise, and he produced many examples to show the existence of an optimum brood size. Under this hypothesis one might expect that in larger broods, each nestling would have obtained a smaller share of the food, and so would have shown a reduced growth rate. This would have led to higher mortality amongst the larger broods, either in the nest or soon after fledging. However, growth rates of nestling Sparrowhawks were independent of brood size (which was mostly in the range three to five) in each of the sub-areas studied. This result, although surprising, was supported by one obtained for another species of raptor by Cavé (1968), who studied the Kestrel in the Netherlands. He found that the mean weights of nestlings at fledging were independent of brood size within the observed range of two to six. Although his results did not support Lack's hypothesis, Cavé suggested that food scarcity might only have become apparent in very large broods (seven or eight young). The same suggestion might apply to Sparrowhawk broods of six or seven nestlings in the areas of good growth.

The results presented here suggested that the amount of prey brought to the nest increased in proportion to the brood size, at least during the first ten days, when the nestlings were brooded by the female and there was no differential heat loss between brood sizes. A study of two Cooper's Hawk nests (Snyder & Snyder 1973) suggested that food was supplied at the same maximum rate irrespective

of brood size. The authors exchanged nestlings experimentally between two nests every two days, and from hides counted the number of prey items and estimated prey weight when brood sizes were alternately two and five. In the first nest, in poor habitat, there was no change with brood size in the number of prey items brought to the nest per day; in the second nest, in good habitat, the increase in the number of prey items brought in when the brood size was five was not significant. However the authors allowed the adult birds only two days to adjust to the changed brood sizes before they were changed again, and even then on each occasion more prey items were brought to the brood of five on the second day than on the first. This suggests that the experiment should have been organised on much longer time intervals, so as to test whether the birds would adjust the rate of bringing prey in proportion to the brood sizes.

Although growth rates were independent of brood size (taken at 6-12 days) even in the central and remote sub-areas of Ae Forest, in these two areas most of the broods were depleted by mortality during the second half of the nestling period. The result was that the mean number of nestlings at fledging, but not at 11 days, was significantly lower here than in the other areas. The pattern of mortality (Table 13) suggested that generally no more than three nestlings could be raised in the remote area and much of the central area, although in one instance all five nestlings were fledged from a central area brood.

In the Annan valley, by contrast, mortality was low, and every brood of five was raised successfully (Table 13). Possibly in this area production of young could have been higher if the clutch sizes, and consequently the brood sizes, had been higher. Evidence collected in the present study does not suggest any explanation why valley females, which laid on average four days earlier than forest birds

(Table 6), did not lay larger clutches than they did, unless they were limited in their food supply at the time of laying. Neither does present evidence explain why females in Ae Forest laid clutches resulting in broods larger than they were able to raise to fledging.

Again the study on the Kestrel (Cavé 1968) showed similar results to those found for the Sparrowhawk. Cavé found that although nestlings in large broods suffered higher mortality than those in small broods, this was more than counter-balanced by the larger initial number of young, so that the largest broods still produced the largest mean number of fledglings.

The present results on growth and survival suggest that the amount of food brought to the nest increased in proportion to the brood size, up to a certain size which was limited by the available food supply. In the remote part of the forest this brood size was three; in the Annan valley it was five or more.

Although hatching was relatively synchronous compared to that of many other birds of prey, a runt system developed with the result that the whole brood did not suffer from competition between the nestlings when food was scarce, since the last nestling hatched was the one most likely to die through competition, and growth rates were also correlated with hatching order. However most runts survived at least twelve days, during which time they depleted the food available for the other nestlings, so it is likely that their presence in most of the remote forest nests contributed to the low growth rates observed there (Table 10). By contrast to the situation found for Sparrowhawks, Scharf & Balfour (1971) found no relationship between growth rate and hatching order in the markedly asynchronously hatching Hen Harrier, but Breckenridge (1935b) mentioned in an American study of the same species that the smallest nestling often failed to

survive. Watson (1957) found a correlation between hatching order and growth rate similar to that found here. His result was from a brood of Snowy Owls (which hatch asynchronously) with relatively poor overall growth.

2.13.3 Habitat quality

Newton (1976) studied Sparrowhawks breeding in the Annan valley and Ae Forest in 1971-3, and found that in the forest the birds started laying later, laid smaller clutches, and produced less young per pair because proportionally more nests failed completely, and there was greater mortality of young even in nests which were successful. In the present study, which overlapped only one year with Newton's, large differences were again found between the same two areas (and more particularly between the remote and central sub-areas of Ae Forest and the Annan valley) in growth rates and mortality of the nestlings, and in the parental care as shown by the presence of the female near the nest. Breeding success, measured in each of these ways, was found to decrease as the remoteness of the nest site from good quality land increased.

The evidence collected suggested that distance from good quality land was linked with a poor local food supply and remoteness from habitats which provided good sources of prey. The low growth rates and frequent mortality due to starvation observed at remote sites suggested that the food supply was limiting. Females were less frequently present near the nest at remote sites when I visited them to measure the nestlings, suggesting that these birds spent more time hunting away from the nest. The consequence of poor parental care at these sites was mortality in wet weather, when the females were not able to protect the young, and also possibly mortality due to predation.

Data on the song-bird populations which were available as prey to the Sparrowhawks will be presented in the following chapter, to make possible further discussion of Sparrowhawk breeding success in relation to the food supply available.

CHAPTER 3

SONG-BIRD CENSUSES

The aims of the census work were (a) to evaluate by use in the field the various techniques available; (b) to use the results from the best technique to compare populations of birds in areas where Sparrowhawks bred.

3.1 Historical: the development of bird census techniques

This review will be restricted to methods for counting and censusing breeding territorial song-birds. All relevant methods published up to the end of 1936 were reviewed by Lack (1937), and some of the later work by Skellam (1958).

The problem, when restricted to territorial birds in woodland, is to assess either absolutely or relatively the numbers of birds of each species. In the woodland habitat they are frequently hidden from the observer, so that most birds are heard rather than seen. The birds' territorial behaviour, particularly their song, makes censusing in woodland possible, but consideration must be given to variations in conspicuousness, both between species and within the breeding cycle of any one species.

The method chosen depends partly on the type of result required: whether it should be an accurate census of bird populations of a defined and necessarily small area, or a sample which will give relative abundances of the different species in a particular area. The methods which have been described fall into two broad categories. In the first, involving mapping, birds are recorded on a map of a defined area, and knowledge of their territoriality makes possible a complete enumeration based on several observations of each male on its territory. Mapping methods are described in 3.1.1. In the second category - line transects or strip surveys - the area studied is essentially

a long narrow belt on either side of the observer as he moves and records all that he sees and hears. The result in its simplest form is a sample which provides information for an assessment of the relative abundance of species, biased by species-differences in conspicuousness. This type of transect will be discussed in 3.1.2. Several authors have adapted this method with the aim of measuring absolute numbers. These methods will be described in 3.1.3. A third category of censuses, in which the observer remains stationary for a fixed time period, has some features of both previous categories. These censuses are discussed in 3.1.4.

3.1.1 Mapping methods

The earliest use of the mapping technique was by Alexander & Alexander (1909), who marked known pairs of summer visitors on a six-inch map (1:10560), counting a single observation of a singing male as a territory. They did not say how many visits they made to their study areas, but they repeated the census for a second year and compared the results.

In some of the transect census methods to be described later, for example Colquhoun (1940a), Howell (1951), a mapping method was used for a complete census of a small area. So little attention was then paid to the mapping method itself that its use was not even described in detail. However with the need for knowledge of absolute densities of woodland birds which became apparent in later years, increased attention was paid to mapping techniques.

Much of the pioneer work was done in Sweden by Enemar (1959), who published a detailed account of his studies in an isolated area of woodland known as Birdsong Valley. He mapped all bird observations made on a series of visits to the valley through the breeding season, each visit requiring a separate map. The records for each

species were then transferred to species maps, and the resulting records, which were often clustered into groups corresponding to territories, were interpreted so as to determine the number of territories for each species within the area. He was also able to estimate his percentage success in detecting each individual territory holder, the "efficiency" for each species being 50-60%. The approach was checked by an experiment in which the author tested his observations against simultaneous records made independently by five other ornithologists. On average each pair of observers had 75% of their records in common.

In 1962 the British Trust for Ornithology (B.T.O.) began a long-term survey of British bird population trends, and they decided to establish plots for this purpose which would be censused annually by the mapping technique. In the pilot survey of 1962 and in the first full year almost all the plots were on farmland (Williamson & Homes 1964), and woodland was included from 1964. Williamson (1964) studied the technique in detail in woodland, and produced results for several species on efficiency (termed "effectivity"), which were generally lower than those of Enemar (1959). The national survey was entitled the Common Birds Census, and observers throughout Britain, most of whom were amateurs, were asked to follow a procedure which differed little from that of Enemar (1959). The rules for mapping censuses were later adopted internationally by the International Bird Census Committee (1969). The Common Birds Census was used by the B.T.O. to set up population indices for many species, the change in the index from year to year being derived from a comparison of the census results. The validity of this index was tested by Taylor (1965). Since 1967 annual reports on bird population changes have been published, e.g. Batten & Marchant (1975).

Several authors have tested the mapping method in the field. Snow (1965) described an experiment in which two independent observers made mapping censuses and a third searched for nests, all on the same farmland plots. The census results varied in accuracy according to the species concerned, with the less conspicuous species requiring a greater number of visits to produce accurate results. The highest estimates of the populations were derived from nest searches; but this was much more easy on farmland than it would have been in woodland. A similar study on three reed-bed species (Sedge Warbler, Reed Warbler, and Reed Bunting), was made by Bell et al (1968), whose census results were poor only for the colonial Reed Warbler. Haukioja (1968) studied the same three species in Finland, and particularly the Reed Bunting. He compared mapping census and line transect results from a population where every nest was known: 75% of the territories were found on 12 visits using the mapping census, but only 40% on 12 line transects. However similar results would not necessarily be obtained for other species, densities, or habitats.

Best (1975) suggested that inconsistency in the mapping method arose not in the field, but in the interpretation of the species maps. He studied a population of Field Sparrows intensively, so that the actual territories of the birds were known, and he also collected mapping census data. Five experienced ornithologists independently interpreted the same species maps. They found population estimates which ranged from 8 to 13 pairs, when the actual number was 15. However Best's example may have been unrepresentative of the method as a whole, since it was hard to interpret for two reasons: the plot was small (2.25 ha); and the density of Field Sparrows was high (667 pairs/km^2 - 50% higher than any single species density found in the current study). Unfortunately Best did not publish the species map concerned.

The problem of inconspicuousness was treated theoretically by Seierstad et al (1965) with particular reference to mapping results. They derived a correction for birds missed by this method. This would however be negligible when eight or more census visits were made, and when the probability of observing a particular territory holder (the efficiency) was over 50%.

Hogstad (1967) made a thorough investigation of the factors influencing census efficiency and, since he was working in coniferous forest, his study is particularly relevant here. He examined survey efficiency for each species (Table 20), and the effects of time of day and weather on the number and type of census registrations. Most species reached a peak level of song activity in the early hours of the morning, and several had secondary peaks in the evening. Wind, especially combined with rain, severely reduced the number of census registrations. Following Enemar (1962), he compared the results of several ornithologists working simultaneously but independently, and found 82% of registrations in common between pairs of observers.

Slagsvold (1973a,b) criticised earlier census work for using restricted census periods and taking little note of seasonal changes in song activity. He found that in an extreme case, the population estimate for the Song Thrush decreased by 50% when the census period encompassed a minimum rather than a maximum of song activity.

3.1.2 Methods for relative abundance

The transect type of census was employed in most surveys made before 1959. The B.T.O. organised a national survey of woodland birds in the late 1930s (Lack & Venables 1939). Observers were asked to record the number of individuals of each species encountered on their woodland walks. The maximum count for each species over a series of walks was coded into three categories, and the mean code

number was used to form an index of relative abundance between species and woodland types. However the method had many shortcomings: the maximum count used depended on the number of walks, the time spent, distance covered on each, and the size of wood, so there was no standardisation between observers.

Yapp (1956a) presented a theoretical approach to the line transect and gave an equation for bird density. This could not however be applied in practice, since several parameters can not be measured. The equation and the mathematical theory behind it were discussed by Skellam (1958). Yapp (1956b, 1959, 1962, 1974) used widely a simple line transect method in which the number of "contacts" with each species was recorded on each transect. The percentage representation of each species was expressed as the relative abundance, and abundances were compared between different woodland types, and in the same area after an interval of 18 years (Yapp 1974). A similar method was widely used by Simms (1971). Their results took no account of the differences in conspicuousness between species and in the same species when in different habitats, and therefore were of limited value.

Watson (1969), working in northern Scottish pinewoods, used the line transect both by single observers and by pairs walking in parallel. He introduced another method, an "area count" in which a number of observers swept through the wood on a broad front, acting as beaters and counting all birds passing through the line. This was considered more accurate than the line transects, although birds could still pass through the line undetected, or could be flushed out of the plot ahead of the line. It was thus biased by differences in conspicuousness between species, and also under-estimated density.

Enemar & Sjöstrand (1967), continuing Enemar's (1959) studies described above, showed that line transects could be usefully employed

to complement the mapping method for species which made up only 2-10% of the total population. Such species might be little recorded on restricted study plots, and line transects could indicate direction, and in some cases extent, of annual fluctuations in the less common species. For commoner species transects were an unnecessary supplement to mapping.

3.1.3 Transect methods for absolute densities

Two extensive studies of Finnish forest birds (Merikallio 1958, Haapanen 1965-6) made use of a transect method. All singing males (and females feeding young) within a strip 25 metres either side of the transect line were counted as pairs, and densities were calculated directly without any corrections, under the perhaps unrealistic assumption that all pairs were detected. This method enabled both authors to cover large areas of forest. Merikallio (1958) extrapolated his results to estimate populations for the whole of Finland, while Haapanen (1965-6) examined bird densities and species distributions in relation to forest soil types and the stages of natural forest succession. However the method which they used was liable to error, due to differences in detectability between species even within the 25 m belt, and also possibly to daily variations in activity due to weather conditions, and breeding behaviour of the birds.

Breckenridge (1935a) devised a transect method in which he recorded the distance of each bird observed from his route. He found that the curve of number of observations plotted against distance from the route increased slightly from zero distance (since some birds moved away from his route before he detected them), and then fell away sharply beyond a certain range. He counted only those observations up to this threshold distance, and assumed that he had counted all the birds within this area. He treated each of the five

commonest species separately, as well as observations of all species combined together.

Colquhoun (1940a) was the first to combine transects with a mapping census of the same area, and he derived as "coefficients of conspicuousness" the factors $\frac{\text{birds per acre (mapping)}}{\text{birds per hour (transect)}}$. His coefficients were misnamed since they decreased as conspicuousness increased, and varied between 0.24 for Chiffchaff and 0.90 for Whitethroat and Mistle Thrush. He found that unit time, rather than unit distance covered, provided the better basis for comparisons between species. These observations were extended to a second year (Colquhoun 1940b).

American workers were interested in the same type of technique, and Howell (1951) modified it for use from a slow-moving car. He also used a mapping method for comparison, so as to derive percentage conspicuousness. This was the percentage of birds which were known by mapping to be within 500 feet (152 m) of the road that were actually recorded from the car on a "roadside census". The resulting values ranged from 1-28% depending on the characteristic behaviour of the species. He was able to cover much of a county of the State of Tennessee on his route, making year-round comparisons for some species and finding annual changes in others. While this method was of value for open-country species, it was less valid for woodland, where most species were relatively hard to detect.

Later theoretical work on transects has considered the relationship between the frequency of observations and the perpendicular distance of the animal from the transect line, with the aim of deriving total numbers within a certain range from the sample obtained on the transect. Eberhardt (1968)discussed various possible equations for this relationship, and Anderson & Pospahala (1970) fitted an equation for frequency against distance to data on duck nests, which enabled

them to make a correction to their observed count. In this particular case, their count of nests over a 16.5 ft (5 m) wide transect had to be increased by 13.5% to make this correction.

Järvinen & Väisänen (1975) used the extensive data from transects in Finland in a further discussion of the relationship between detectability and the distance from the transect route. They estimated the parameters of their models from the percentages of observations which were made within the "main belt", that is within 25 m of the transect line. They concluded that corrected transect results could be important in the estimation of densities of rare species, in monitoring long-term fluctuations, and in the analysis of species diversity. However they pointed out that transects should not be used in the estimation of absolute densities.

The principle underlying the method of Emlen (1971) was an extension of that of Breckenridge (1935a). It will be described in detail later (section 3.5.1). Emlen (1971) calculated densities directly from transects in which the distribution of observations away from the transect route was recorded. He corrected for differences in detectability, and obtained further correction factors by comparison with a mapping census on a particular area, so supposedly making full allowance for differences in conspicuousness between species.

3.1.4 Fixed-time counts

A modification of the line transect technique involves the recording of bird contacts either seen or heard from one point in a series of short time intervals of fixed duration, usually 10-20 minutes. These were called "time quadrats" by Yapp (1962, 1974), who used them in conjunction with transect studies. In this case he recorded the species detected in each time period, and then calculated for each species the percentage of periods in which it was detected. This

was analogous to transect measures of relative abundance, and gave him similar results. However he did not count the number of individuals of each species encountered in each time quadrat, so the method was insensitive to differences in density. The same method was used by Gibb (1960) as a check when making counts of flocking birds in pine plantations in winter. Krzanowski (1964) developed a method which combined some features of transects with fixed time counts. He made two-minute stationary counts of all birds detected from one point, and then moved beyond the range of these individuals before making the next two-minute count. He then calculated the mean number of birds of each species detected per two minutes.

The fixed time census method has been studied to greatest extent in France (Blondel et al 1970). The observer remained stationary during the period of 15 or 20 minutes, and counted all birds heard or seen, using direction to distinguish individuals. The authors derived densities from their results, and compared these with densities from a mapping method to obtain correction factors for each species. Because this technique sampled a relatively restricted area, they recommended it as particularly useful in habitats of limited extent, for example hardwood areas within conifer forests.

3.1.5 Census methods chosen for evaluation

Several representative methods from among those described were selected in the present study for evaluation in the field, namely:

(a) the mapping census (Enemar 1959, Williamson 1964),

(b) the simple line transect (Yapp 1962),

(c) the complex line transect (Emlen 1971),

(d) the fixed time count (Blondel et al 1970).

The roadside census (Howell 1951) was thought inappropriate for inconspicuous birds in dense woodland, and the area count (Watson 1969) could not be conducted by one observer working alone.

3.2 The census plots

In all, 17 plots were censused in one or more years during 1973-5 (Table 18). The Dumfries plots (Figure 2) included six in hill spruce plantations (four in Ae Forest and two in Greskine Forest), and one in hill larch plantation in Ae Forest (Table 19). There were six plots in the Annan valley, Dumfries, comprising two in pine plantations, two in semi-natural scrubby birch/pine woods regenerating on drained peat moss, a small semi-natural mixed wood, and an area of riverside scrub. The Spey valley plots (Figure 3) included one of semi-natural pine, two in planted pine, and one in semi-natural birch (Table 19). Line transects were made on seven of these plots. The total of 31 mapping censuses was spread over the three years, and the nine series of transects were mainly in 1973 (Table 18).

All the plots were in woodland or scrub, and none in open areas, because evidence from prey remains and a radio telemetry study (Newton & Marquiss, in progress) showed that Sparrowhawks spent almost all their time when hunting in woodland or on wood edges. Each of the plantation plots was chosen to be as uniform as possible. The plot locations were further constrained by timber operations and by problems of access, but the total samples of woodlands censused were representative of those which occurred in the two study areas.

Diagrams of the vegetation profiles of each census plot were constructed (Figure 14), so that the diversity of the foliage structure could be calculated and compared with the diversity of bird species, following MacArthur & MacArthur (1961). Vegetation profiles were however defined and measured differently to the MacArthurs' method: the maximum and minimum foliage heights were measured optically, using a hypsometer. The height at which the canopy was most widespread was also measured, and the percentage of the ground covered by the canopy

TABLE 18 - PLOTS CENSUSED IN EACH OF THREE YEARS, 1973-5.

Used for:	Plots:															
	A1	A2	A3	A4	A5	G1	G2	T	W	K	H	D1	D2	S1	S2	S3	S4
Mapping 1973	x	x	x	x		x	x							x	x	x	
Mapping 1974	x	x	x	x						x	x	x	x	x	x	x	
Mapping 1975		x	x		x			x	x	x	x	x	x		x		x
Transects 1973	x	x	x	x										x	x	x	
Transects 1974		x	x														

Note: Prefix A denotes Ae Forest, Dumfries-shire,
" G " Greskine Forest, Dumfries-shire,
" S " Spey valley, Inverness-shire,
and other letters are used for other plots in the Annan valley, Dumfries-shire.

TABLE 19 - DETAILS OF THE CENSUS PLOTS: SIZE, SITUATION AND VEGETATION.

See Figures 2-3 for locations and Figure 14 for vegetation profiles.

Plot	Area (ha)	Altitude (m) Aspect	Land Class	Dominant Tree species	Planting date Age when censused	Vegetation: Ground layer	Vegetation: Shrub layer	Vegetation: Adjacent areas	
Ae Forest, Dumfries-shire									
A1	11.1	210-260 SW	8	10.6 ha Sitka Spruce 0.5 ha larch	1927 46-47	Sparse	None	Rough grazing to west	At western edge of forest. 2.4 ha spruce wind-blown in 1974, left lying, providing abundant ground cover.
A2	9.2	210-275 W	6/8	7.5 ha Norway Spruce 1.2 ha Sitka Spruce 0.5 ha larch	1938 35-37	Brashings and fallen trees	None	Spruce forest	On a hillside
A3	10.2	260-300 SE	8	4.1 ha Norway Spruce 6.1 ha Sitka Spruce	1940 33-35	Sparse Brashings and fallen trees	None	Spruce forest	On hilltop
A4	5.8	135-210	6/8	5.0 ha Japanese Larch 0.6 ha Norway Spruce 0.2 ha Scots Pine	1946 27-28	Sparse brashings, grass	None	Valley pasture below lowest corner	Spruce and pine formed several 'islands'. A few scattered Ash and Alder remained from before forest planting.

TABLE 19 (continued)

A5	10.9	300-365 W	8	Sitka Spruce	1953 22	None	None	Similar plantation	Plantation at 'thicket' stage. Could be penetrated only along narrow unplanted rides approx. 50m apart.
Greskine Forest, Dumfries-shire									
G1	8.8	275-335 E	8	8.0 ha Sitka Spruce 0.8 ha wind-blown in 1968	1941 32	Brashings Mainly cleared	None	Spruce forest, extensive wind-blown area to S.	On a steep hillside.
G2	7.3	210	8	Norway Spruce	1942 31	None	None	River and rough grazing to E, open strip containing railway line to W.	On flat valley floor, between river and railway.
Annan valley woods and plantations									
T	12.4	75	6	Scots Pine	1932 43	Calluna, grass, Bramble in parts.	None	Pine plantation	At centre of 1km^2 pine plantation.
W	11.9	60	4	Scots Pine	c.1935 c.40	Calluna, mosses, grasses. Bramble dense in parts.	Hedgerows of Beech and Hawthorn on N. and W. boundaries	Arable fields and hedgerows to N, pasture to W, cleared plantation to S.E.	On a corner of 1km^2 pine plantation.

TABLE 19 (continued)

K	9.5	75	4	Birch/Scots Pine intermixed	1945*	Calluna in open parts, sedges.	Birch scrub in parts.	Mature Scots Pine clumps, arable land to N. & E. Deciduous wood to S.E.	Originally used for peat cutting. An additional 3.9 ha predominantly open with scattered scrub was censused.
H	12.0	45	4	Birch/Scots Pine intermixed. 0.3 ha mature Norway Spruce	1945*	Calluna in dry areas, sedges where wet.	Birch scrub in parts.	Marshy fringes of loch to N.E., wood to N.W., pasture.	Originally used for peat cutting. An additional 2.2 ha predominantly open with scattered scrub was censused.
D1	4.3	70	4	Mixture: Birch, Oak, Ash, Sycamore, Beech, Norway Spruce, Scots Pine.	Semi-natural	Grasses, herbaceous plants	Varied: saplings of broad-leaved trees; rowan, honeysuckle	Pasture on all sides except NE corner (Spruce plantation)	1 ha W. of minor road more open than the remainder, with a small rookery (10 nests) in Scots Pines.
D2	3.6	70	4	Alder dominant in parts. 2.1 ha open grassy pasture also censused.	Semi-natural	Grasses, herbaceous plants	Gorse, Salix spp. Broom, Hawthorn.	River to W. arable and pasture to E.	A mixture of habitats on the bank of Ae Water: stream edge Alders, with dense scrub on shingle banks; pasture with a marshy pool and sedge bed; further E. a bank and strip of open Gorse and Hawthorn scrub, and a secondary stream.

* Approximate start of regeneration.

TABLE 19 (continued)

Spey valley

S1	8.7	250-290 NE	8	Scots Pine of all ages.	Semi-natural	Dense Calluna and Vaccinium	Clumps of Juniper	Planted and semi-natural pinewoods.	On gentle hill slope.
S2	11.7	240-290 NE	8	c.7 ha Scots Pine c.5 ha Lodgepole Pine intermixed at boundary.	1932 41-43	Sparse Calluna and Vaccinium	Scattered Junipers	Planted and semi-natural pinewoods.	Close to plot S1
S3	8.8	230	8	Birch of varying heights.	Semi-natural	Calluna and grasses where dry; Bog Myrtle and sedges where wet.	Birch scrub, few Juniper clumps, Bird Cherry.	Dry birch wood to E. & S.; moorland to N. & W.	Grazed by sheep.
S4	13.7	335	8	Scots Pine	1926 49	Calluna throughout.	None	Pine plantation.	In Queen's Forest, Glenmore.

FIGURE 14 - VEGETATION PROFILE DIAGRAMS OF THE CENSUS PLOTS.

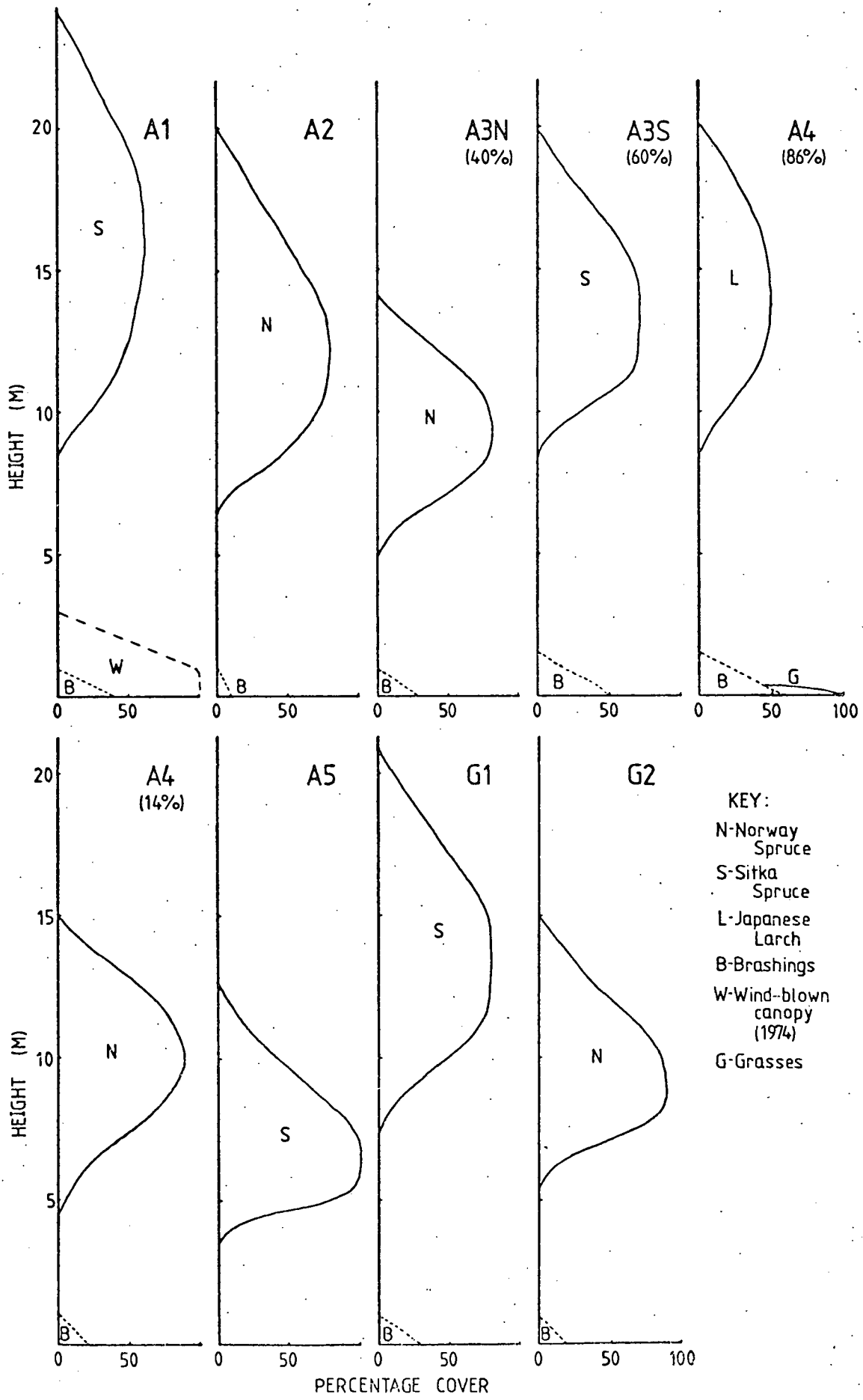


FIGURE 14 (continued)

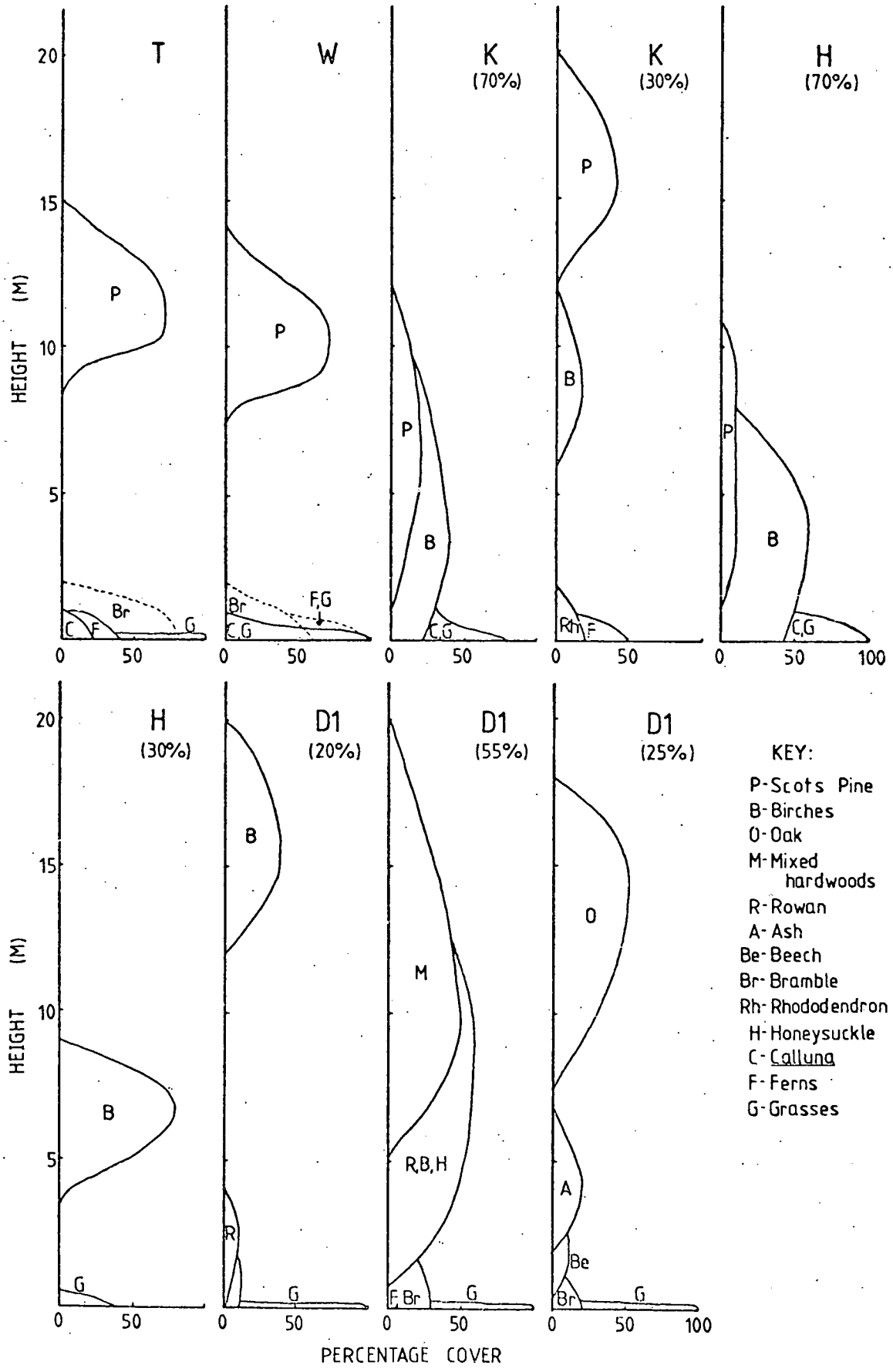
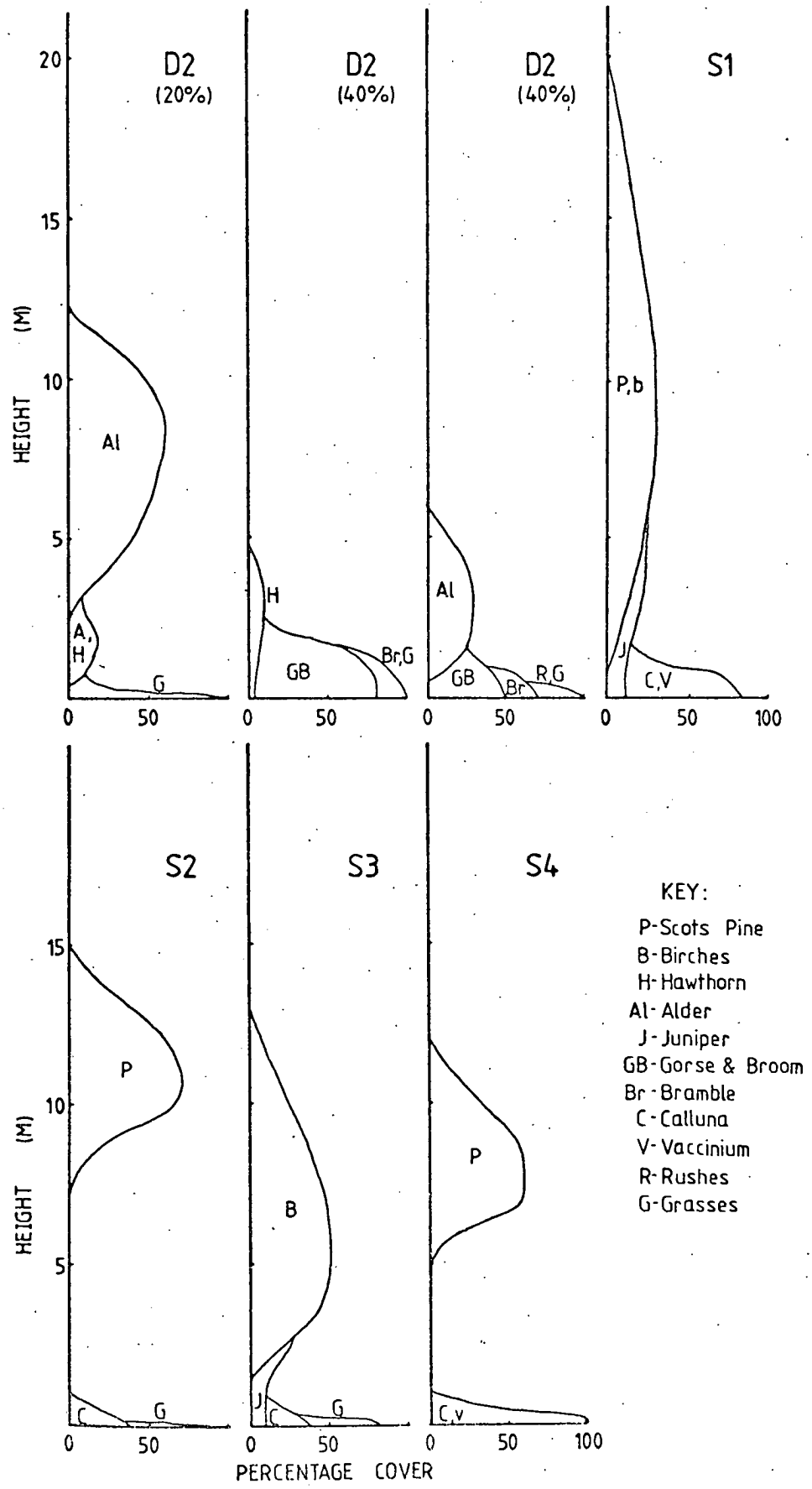


FIGURE 14 (continued)



was estimated visually to the nearest 10%. A profile of the canopy was sketched using its upper and lower limits and the maximum percentage cover as guide points. The same procedure was followed for any understorey layers which were present, including the ground layer. Dead branches and ground cover of brashings, often extensive in spruce plantations, were excluded. In plantations, tree heights were uniform, and measurements at one or two points sufficed. On the more natural plots, where tree heights varied, more points were surveyed, and the vegetation profiles were smoothed to include the range of heights. When a plot contained two or more distinct vegetation types, separate profiles were drawn for each one. These were amalgamated later in proportion to the area of each type found on the plot.

Thus on plot A2 (Figure 14 ii) the canopy extended from 6.5 m to 20 m, and was densest (covering 80% of the horizontal plane) at 12 m. Brash up to 1 m high covered 20% of the ground. On the main scrub area of plot K (Figure 14 xii), pines and birches up to 12 m high covered 40% of the ground, and extended down to ground level. Calluna and grass up to 1 m high covered a further 60% of the ground. Figure 14 should be interpreted as a set of diagrammatic representations of the vegetation of the plots, derived as described above. It was thought to be unnecessarily time consuming to make measurements of foliage density at a series of heights, as were made by MacArthur & MacArthur (1961), when profiles could be constructed quickly from a few key measurements, as described above.

The profiles were divided into a number of height ranges, and the areas within each range were calculated directly from the diagrams (Figure 14). The proportions p_i of the foliage within each range were found, and the foliage height diversity was calculated for each profile by the Shannon & Weaver (1949) formula: $F.H.D. = -\sum p_i \log_e p_i$.

This formula for diversity took account both of the number of ranges observed in each area and of the evenness of the distribution of foliage between them (Pielou 1969). Several possible divisions into two, three, and four ranges were used, and following MacArthur & MacArthur (1961), one was selected which maximised the correlation between the diversities of bird species, calculated from mapping census results, and of foliage heights (see p.151 and Figure 22). There were several divisions into two, three and four ranges for which $r > 0.8$, but the maximum correlation ($r = 0.932$, 16 d.f., $P < .01$) was obtained with four height ranges: 0-0.6 m, 0.6-6.0 m, 6-15 m, >15 m. These corresponded approximately to herb, shrub, lower canopy and upper canopy layers.

By a similar selection process, MacArthur & MacArthur (1961), working in temperate North America, chose ranges of 0-2 ft, 2-25 ft, > 25 ft (0-0.61 m, 0.61-7.62 m, >7.62 m). Diversities from tropical areas were best correlated when two or four ranges were used (MacArthur et al 1966). The improvement of the ranges used over some of the choices of three and two ranges was only a small one, and so no significance should be attached to the number of ranges chosen.

3.3 The mapping census

3.3.1 Method

The plots, which were described in the previous section, were chosen to be approximately ten hectares in area, and as uniform and with as little edge as possible. Using ranging poles, measuring tapes, and a prismatic compass, each plot was marked out with a 50 m grid. Trees at the intersections of grid lines were marked with red plastic tape, and labelled with a grid reference. A map of the plot on a scale of 1:2000 was drawn, with each taped tree shown, so as to make possible an accurate fix of a ground position on the map.

The field procedure was in accordance with the IBCC (1969) recommendations. On each visit a fresh map of the plot was carried and all birds heard or seen were identified and marked as accurately as possible. A two letter code was used for each species, and using conventional symbols each activity was distinguished, as follows:

(GC) Goldcrest singing.

CH♀ Chaffinch heard (not singing), or seen, and sexed when possible.

(WR)=(WR) Two Wrens singing simultaneously. (Only used for birds of the same species.)

ST → ST Song Thrush moving position; the arrow was marked with ? if movement of a single individual rather than the presence of two birds was suspected, but not certain.

←SI← Siskin flying overhead.

(RO)(RO) Aggressive encounter between two Robins.

BB Blackbird alarm calls.

WW* 5e Willow Warbler's nest with 5 eggs.

See Figures 15-16 for examples of visit maps.

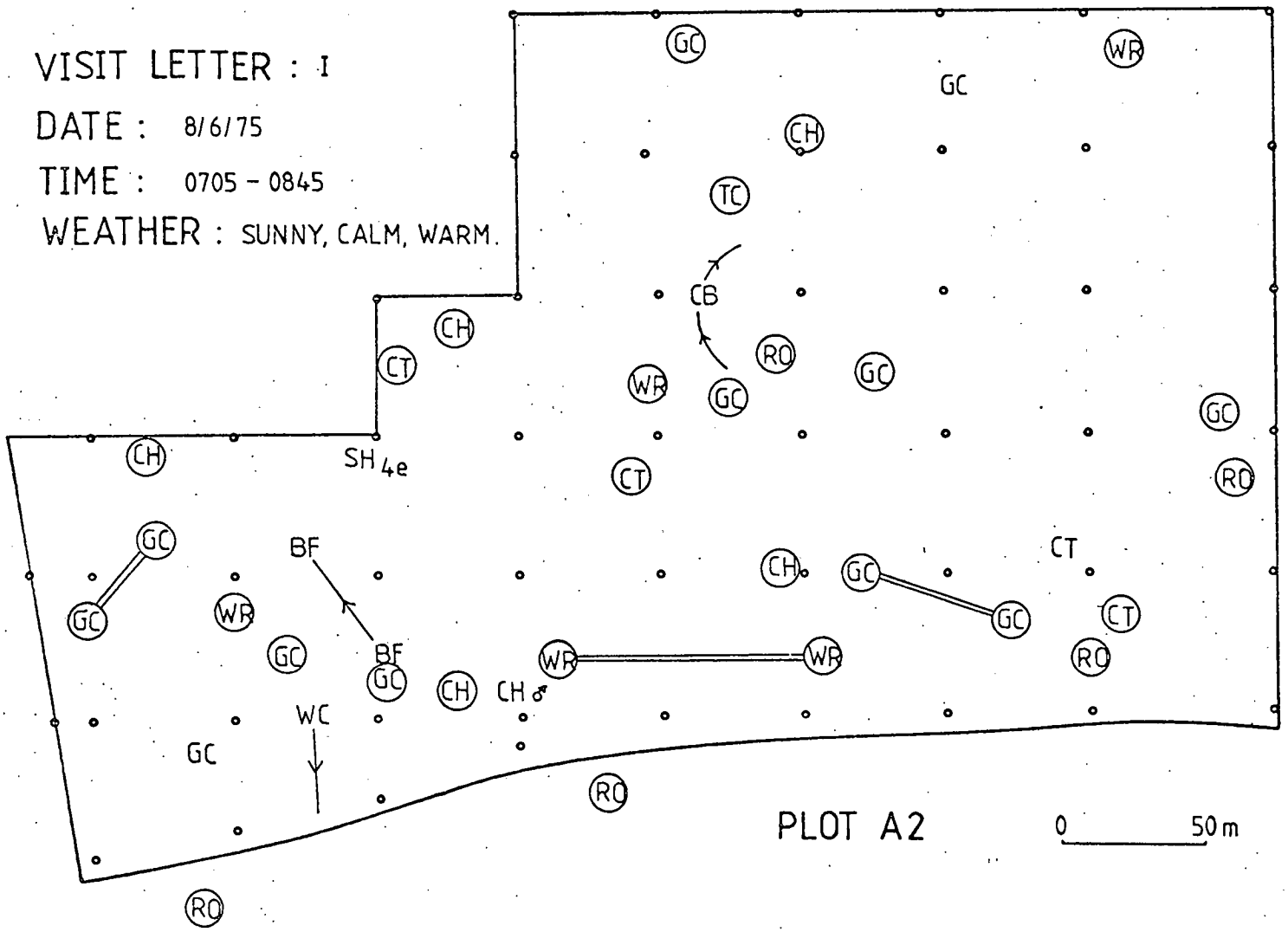


FIGURE 15 - AN EXAMPLE OF A CENSUS VISIT MAP

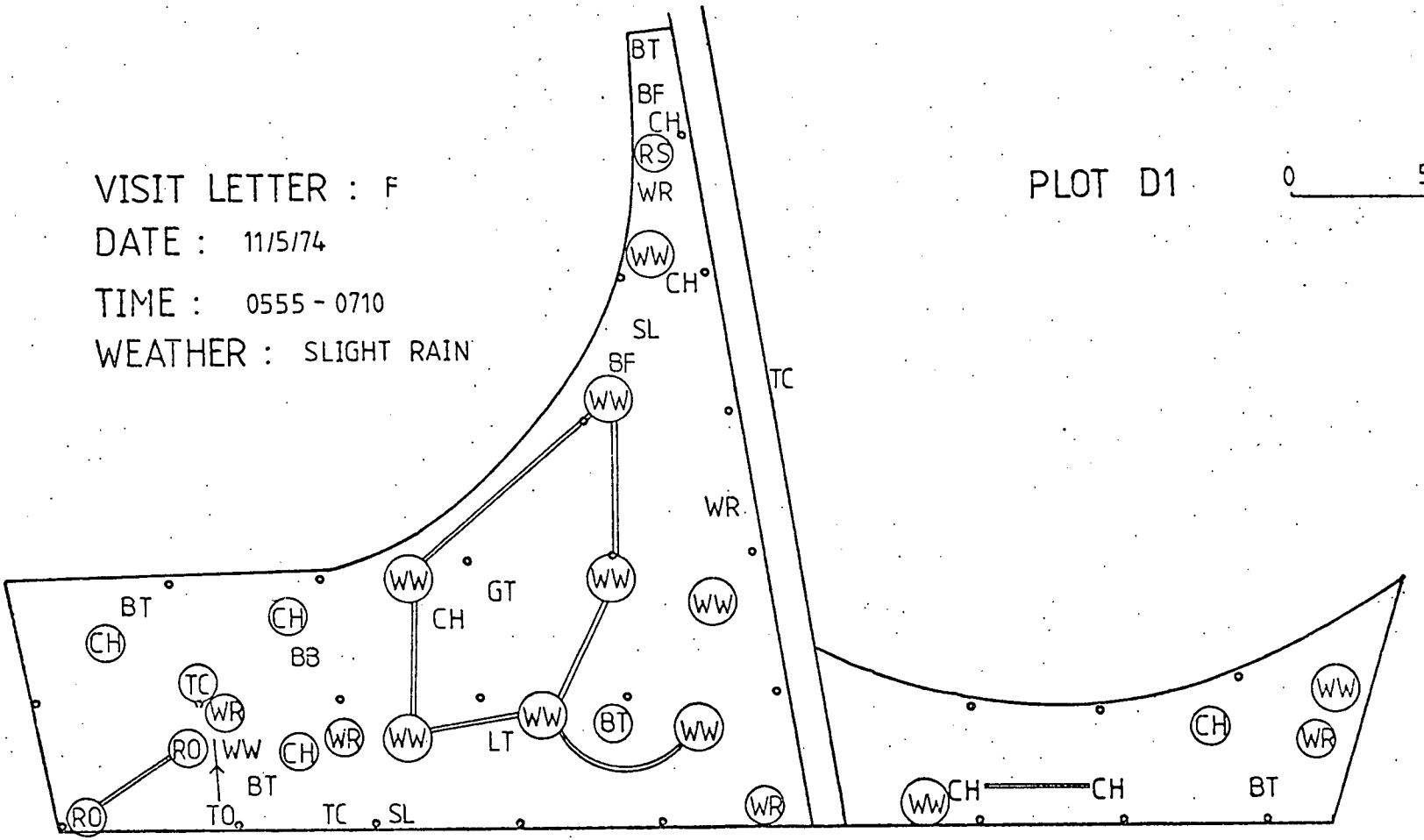


FIGURE 16 - AN EXAMPLE OF A CENSUS VISIT MAP

Plots were covered systematically on each visit, usually by following parallel rows of marked trees, such that no point of the plot was more than 25 m from the route followed. The direction of travel along the route was different on each visit from that on the previous one. Stops were made when a bird was detected so that its position could be determined and marked on the map; additional stops were made frequently so that any active bird would be heard. In the densely planted plots it was impossible to see birds beyond a short distance, and detection then relied almost entirely on sound. Estimation of range was correspondingly more difficult on these plots. There was however no problem in the application of the mapping or any other census method in identifying each species by its song or calls, which were distinctive and easily recognised.

No time limit was set, and visits generally took about two hours, depending on the size of the plot and level of bird activity. The visits were made in the first five hours after sunrise, when most species reach a peak of song activity (Hogstad 1967). Visits to two different plots were usually made on each morning, and at each plot visits alternated between first and second of the day. No visits were made in moderate or heavy rain, or in strong wind. Palmgren (1930) found that heavy rain and strong wind among other factors inhibited song, and Hogstad (1967) estimated that registrations were cut by 45% in strong wind, and by 80% when wind and rain occurred together.

On each visit the date, time of start and finish, and weather were noted. A total of 10 visits was made to each plot in 1974-5, (but only 8 in 1973), since Hogstad (1967) and IBCC (1969) had recommended 10 as a minimum number of visits in closed woodland. Visits were lettered consecutively A to J (H in 1973). The censuses were made throughout late March to mid-June, and so covered the period of

maximum territorial activity (prior to laying) for most passerine species. All phases of the "song course" described by Slagsvold (1973a) were thus included, so his criticisms (Slagsvold 1973b) of studies made during a limited period did not apply, except possibly to the two Spey valley censuses in 1975, which spanned a period of only 25 days.

At the end of the field season, species maps were constructed from the visit maps. For each species, all registrations were transferred to the same location on the species map, the species code being replaced by the visit letter (see Figures 17-19 for examples). The species maps were interpreted using the following IBCC (1969) rules to determine the numbers of territories on each plot:

1) Each cluster of observations required at least three registrations to be a valid territory (but only two for summer visitors which were only present in the area for seven or fewer visits; this applied in only a few cases, e.g. for the uncommon Garden Warbler).

2) A pair of simultaneous song observations could not lie within the same territory.

3) No more than two double registrations (that is, two records on the same visit but not simultaneous) could lie within a single territory.

Using these rules, the species maps were divided by approximate territory boundaries. Surplus registrations occurred both outside territories and as double registrations. These were assumed to arise either from migrant individuals, or from birds unable to gain a territory or mate and so not breeding.

Territories at the edges of the plots required special treatment. Birds detected up to 50 m outside the plot boundaries were also marked on the visit maps, so that the species maps could include territories

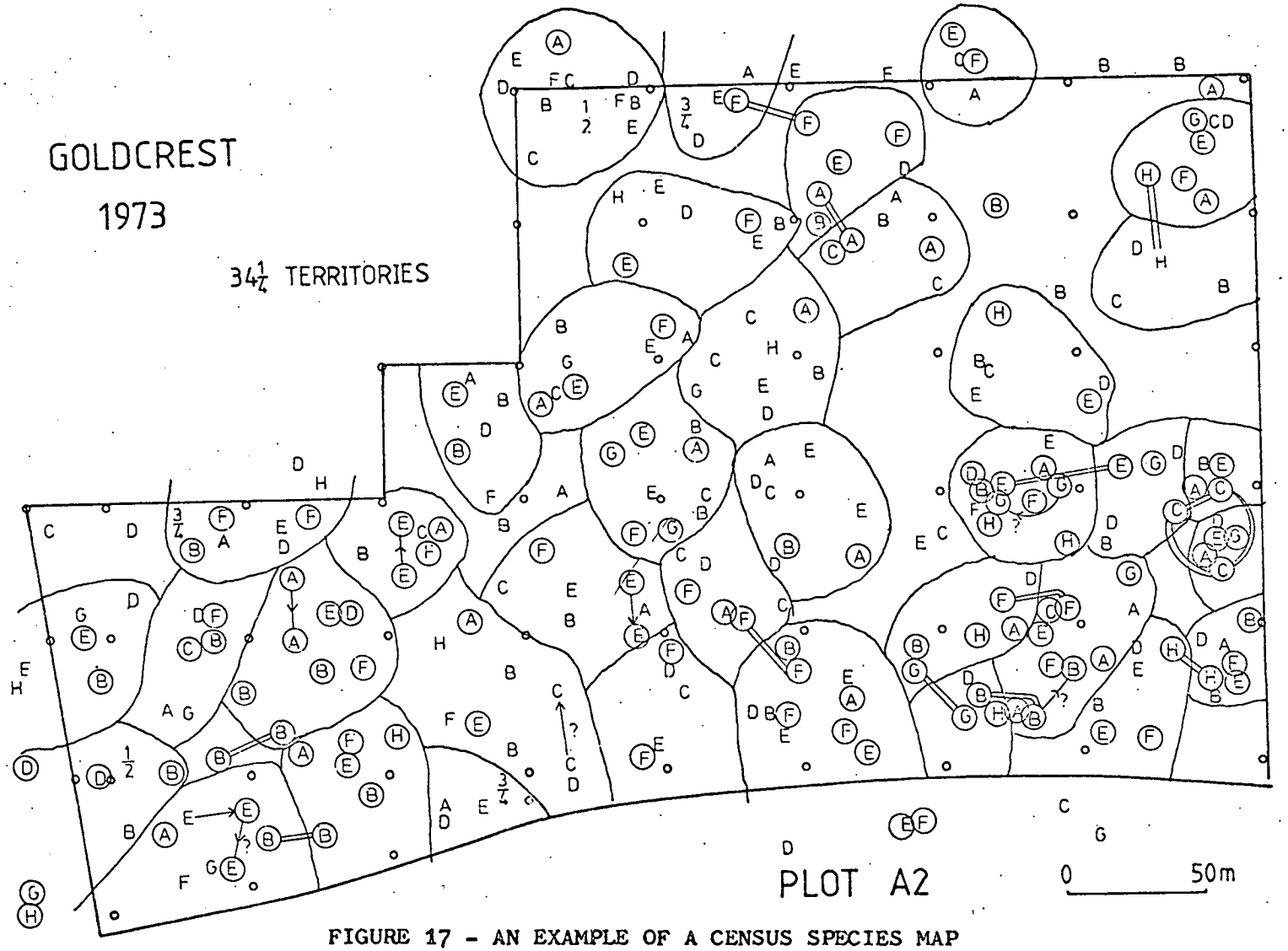


FIGURE 17 - AN EXAMPLE OF A CENSUS SPECIES MAP

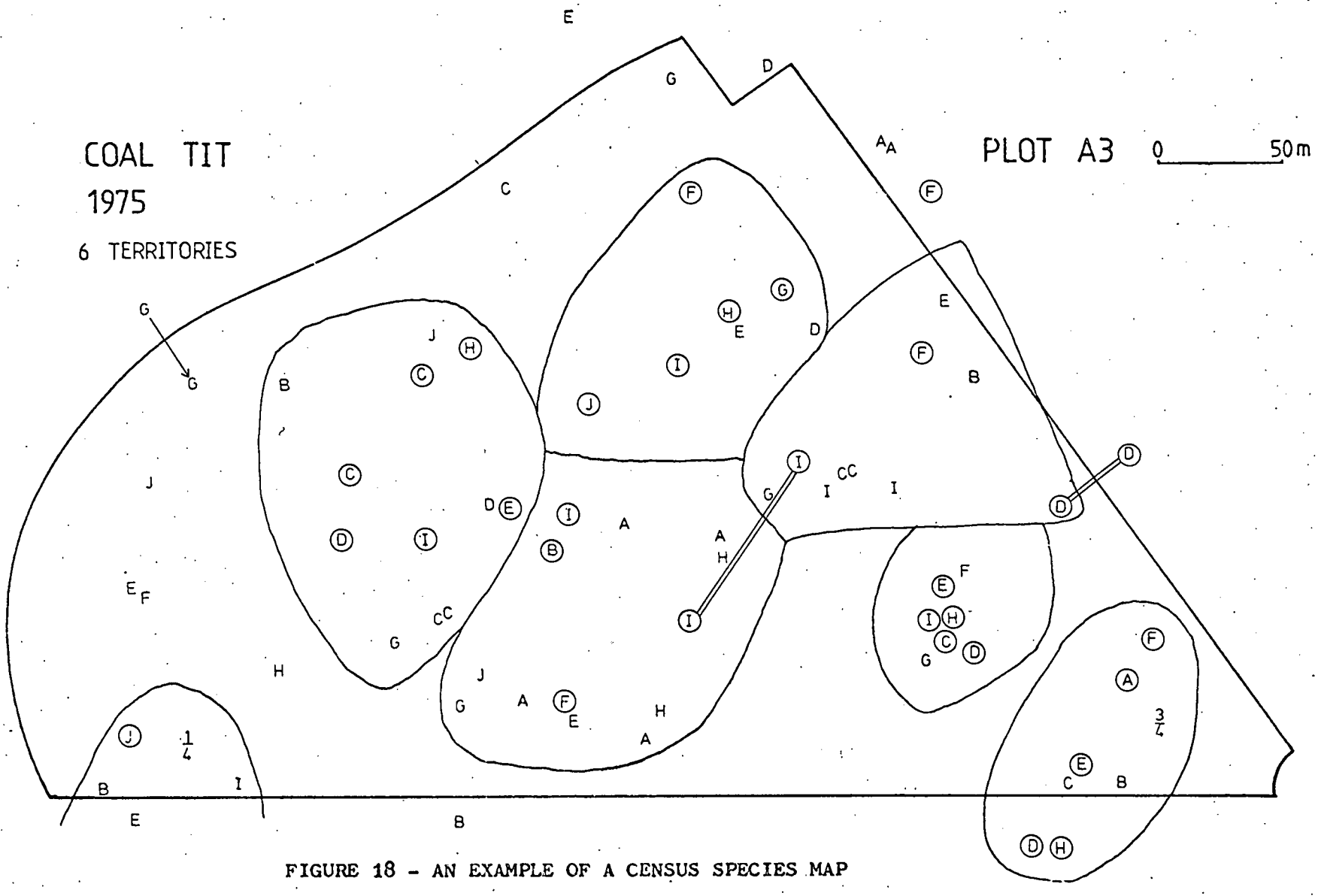


FIGURE 18 - AN EXAMPLE OF A CENSUS SPECIES MAP

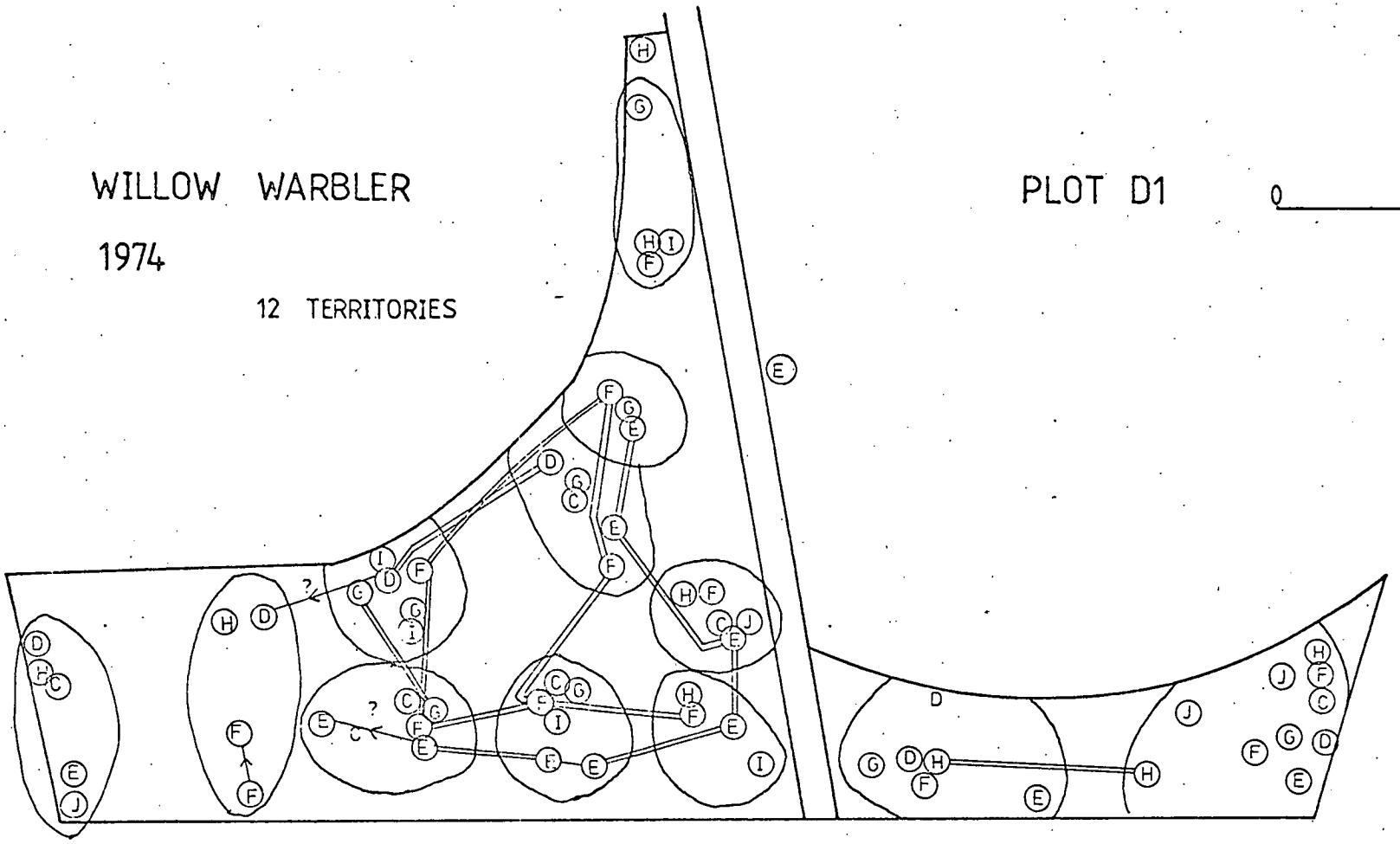


FIGURE 19 - AN EXAMPLE OF A CENSUS SPECIES MAP

partly in the strip surrounding the plot. Then, according to the proportion of registrations which fell within the plot boundary, a fraction, in quarters, of that territory was allocated to the plot. This procedure differed from that of the IBCC, where an edge territory was counted as zero or one, according to the proportion of registrations within the plot. The counting used here made possible greater sensitivity, especially for sparsely distributed species.

After the completion of the 1975 season, all the species maps from 1973 and 1974 were interpreted again together with those from 1975, so as to standardise the analyses as far as possible, particularly in the ambiguous types of situation where observations were diffusely scattered. In some cases the 1975 interpretations differed slightly from those obtained in the previous years, and it is the figures derived from the later re-analysis which are used here. Some of the maps were also given to other people together with the rules to be followed for their interpretation, and the results were compared.

When each species map had been interpreted, the number of territories was divided by the plot area in km^2 to give the density for each species, expressed as a standard in pairs per square kilometre. The diversity of the species composition found on each plot was calculated from the Shannon & Weaver (1949) formula: $D = -\sum p_i \log_e p_i$, where p_i = proportion of the total represented by the i th species, and the sum was taken over all species. The diversity increased both with the number of species found (S) and with the even-ness of their distribution; for example four species which each formed 25% of the total would have had $D = \log_e 4 = 1.386$; ten species each forming 10% of the total, $D = \log_e 10 = 2.303$, and if there were ten species distributed with percentages of 50, 20, 10, 5 and the remainder 2.5, the diversity would have been 1.602. The even-ness of each

distribution, $J = D/\log_e S$ (Pielou 1969) did not give useful comparisons between plots because the value of S was dependent on the number of relatively scarce species whose presence was recorded on the plots which were assigned estimated densities. These species had very little effect on the values of D, but directly affected the values of J.

Full results (Table 31) follow in section 3.7; the remainder of this section concerns the evaluation of the mapping method, and in particular two possible sources of error in its application.

3.3.2 Inconspicuousness of certain species

Census efficiencies (see p.83 for explanation) were calculated so as to compare the conspicuousness of different species, and to estimate the proportion of birds which might have been recorded too seldom to quality as territory holders in the interpretation of species maps (i.e. less than three times). Efficiency was defined following Hogstad (1967), as the percentage of potential registrations of the stationary population actually made, and was an estimate of the percentage chance of recording a given individual on a single visit. Unlike Williamson's (1964) definition of efficiency, each bird was assumed to be available on every visit, with the obvious exception of summer visitors before their arrival. All territories counted as completely within the plot were included; for example there were estimated to be five complete Chaffinch territories on plot S1 in 1974, giving a total of 50 potential registrations in ten visits. 37 registrations were actually made in these territories, an efficiency of 74%. When there were five or more territories on a plot the standard error of each efficiency was calculated from the standard deviation of the number of registrations made in each of the territories.

Efficiency depends on the number of territories drawn on the census map, so an apparently low efficiency might result from too great a number of territories. This impinges on the problem of species map interpretation, to be discussed in the next sub-section.

The efficiencies in different woodland types were in broad agreement (Table 20). The 1973 figures, based on only eight visits to each plot, were generally slightly higher than those for later years, but were not strictly comparable, so only 1974-5 values were used. A few anomalies were noted: the value for Chaffinch in Ae plots was significantly lower than the others, as was that for Coal Tit in the Annan valley plots. Most of the efficiencies were close to those found by Hogstad (1967), except for Coal Tit and Willow Warbler.

Some aspects of census efficiency can be examined theoretically (Table 21). If it is assumed that the true probability of detecting an individual bird is constant, than the probability of its being registered as a territory holder, that is being detected on three or more visits, can be calculated using the binomial distribution. The expected estimate of the efficiency can be calculated, since inconspicuous birds would be missed under the rules for determining territories, so biasing the efficiency estimates. The minimum efficiency that could be recorded was 30% (37.5% in 1973).

In 1973, when only eight visits were made to each plot, as many as 15% of territories could have been missed because their holders were recorded too seldom. In the later two years, ten visits were made, and on application of the efficiency estimates (Table 20), no more than 5% of territories would have been missed in the case of the least conspicuous species, the Goldcrest, and less than 1% for the most conspicuous, the Wren.

TABLE 20 - EFFICIENCIES CALCULATED FROM THE MAPPING CENSUS METHOD.

Efficiency = percentage probability of recording an individual on its territory during a single mapping visit. Standard errors and the numbers of complete territories concerned (N) are given.

Species	1974/5[1] Ae Forest spruce plantns.		1975 Annan valley pine plantns.		1974/5[1] Spey valley pine plantns.		1974/5 Annan valley broad-leaved		Hogstad (1967)	
	N	eff.	N	eff.	N	eff.	N	eff.	N	eff.
Goldcrest	132	56±1	8	56±4	10	49±3	15	52±4	32	50±4
Chaffinch	32	54±2	12	63±4	16	67±4	62	63±2	66	69±2
Wren	33	70±3	17	68±4	-		66	63±2	11	62±4
Coal Tit	22	65±2	10	62±3	9	67±5	19	48±3	13	54±5
Robin	-		5	50±7	-		56	56±2	71	57±2
Willow Warbler	-		-		-		112	67±1	32	76±2

[1] 1973 censuses are excluded because they were not comparable (see text).

TABLE 21 - THEORETICAL ASPECTS OF EFFICIENCY IN THE MAPPING CENSUS.

Given certain true probabilities (p) of an individual record on a territory, theoretical probabilities are given of failing to register the territory because three records were not made, together with the resulting biased expectations of the efficiency to be observed.

Actual p	Probability that territory is missed given 8 visits	10 visits	Expected estimate of observed value of p 8 visits	10 visits
50%	14.5%	5.5%	54.8%	51.9%
60%	5.0%	1.2%	62.0%	60.5%
70%	1.1%	0.2%	70.4%	70.1%

3.3.3 Difficulties in the interpretation of the species maps

The difficulty in interpreting species maps varied with density and species (Table 22). In general Wren and Willow Warbler, which were the species with the highest efficiencies, were also the easiest to interpret; Goldcrest and Coal Tit were the most difficult, and Chaffinch and Robin were intermediate. Williamson (1964) also noted the existence of 'difficult' species, such as Blackbird and Dunnock.

When interpreting the maps, in cases where clusters of registrations were not apparent, observations were grouped into supposed territories of a size which took note of the observed distances between birds singing simultaneously on the plot as a whole, and which generally grouped together as many adjacent observations as possible without double registrations (p.106) within the same territory. For example, a diffuse group of eight song records would have been joined as one territory, provided they did not cover too large an area, although it would have been permissible within the rules of interpretation to group them as two territories with four records each. The procedure adopted would have resulted in minimum estimates for density throughout. A thorough personal knowledge of the plots often made it easier to interpret the maps than it would have been for a person other than the field observer, as was mentioned by Best's (1975) collaborators.

In a more limited similar test to that of Best (1975), a sample of my 1973 species maps was interpreted by Mr L A Batten, who is experienced in such work with the B.T.O. populations section. The results of his interpretation, compared with my own in 1973, and again in 1975 (Table 23), suggest considerable divergence in interpretation, which was not consistently in the same direction. In the Coal Tit and Blue Tit, the discrepancies probably arose from the less precise

TABLE 22 - CHARACTERISTICS OF THE SPECIES-MAPS FOR THE COMMONER SPECIES.

+ = high - = low 0 = average n/a = not applicable

Species	Example	Frequency of clustering of observations	Frequency of simultaneous songs	Tendency for diffuse observations at low densities	Tendency for dense uniform observations at high densities
Goldcrest	Fig. 17	-	-	+	+
Wren		+	+	-	n/a
Coal Tit	Fig. 18	-	-	+	n/a
Robin		0	+	0	n/a
Willow Warbler	Fig. 19	+	+	-	-

Chaffinch varied between and within plots, with good clusters of observations and simultaneous songs in parts, but with diffuse groups, often with few song records, in other parts.

TABLE 23 - COMPARISON OF NUMBERS OF TERRITORIES FOUND BY THE AUTHOR IN 1973, AND AGAIN IN 1975 FROM THE SAME SPECIES MAPS, WITH THE INTERPRETATIONS OF L. A. BATTEN.

	A2 Goldcrest	S1 Chaffinch	A4 Chaffinch	A2 Coal Tit	S3 Blue Tit	A1 Wren
D.M. 1973	38	$6\frac{1}{2}$	$3\frac{3}{4}$	$3\frac{3}{4}$	$3\frac{3}{4}$	6
D.M. 1975	$34\frac{1}{4}$	$5\frac{3}{4}$	$4\frac{3}{4}$	$4\frac{1}{4}$	$3\frac{1}{2}$	$6\frac{1}{4}$
L.A.B.	32	7	$4\frac{1}{2}$	6	6	6

B.T.O. treatment of edge territories, and the lack of knowledge of the plot, respectively. The Goldcrest map (Figure 17) was the most notable of those consisting of a dense, uniform cover of the plot and, with greater experience, my own 1975 estimate was closer to Mr Batten's than was my 1973 one.

Since the object of the census work was comparison of bird densities in different woods, consistency in the method was the most important requirement. For this reason, all the census data quoted derive from a re-interpretation of the species maps made in autumn 1975, in which the guidelines for un-clustered observations described above were used. Thus all the censuses were performed by the same person, who used the additional knowledge of the plots to interpret all the species maps within a short space of time. Because the method was standardised, results could be compared between plots which differed widely in structure and so in conditions for observing birds.

The mapping method did not permit of any way to estimate the magnitude or direction of error in its use. However despite the drawbacks discussed above, the basic principle of the mapping method was the most reliable one available, because it was applied in a consistent manner, and it gave an intensive survey of a stationary population over most of the breeding season.

3.4 Simple line transects

3.4.1 Method

Line transects were made in 1973-4 on some of the plots used for mapping census (Table 18). The data used to evaluate simple line transects were taken from the same field visits as the complex line transects, described in the following section. The information required for simple transects was the number of contacts (visual or auditory) with each species recorded on each visit. These were expressed as percentages of the total numbers of contacts, termed "relative abundances" by Yapp (1962), either for each transect or, when summed, for a series of transects on a plot over a season. No densities could be calculated using these transects, since Yapp's (1956) equation for density involved parameters which could not be estimated.

3.4.2 Results

Since the transects were made on the same plots as the mapping censuses, relative abundance figures could be compared between the two methods (Table 24 and Figure 20). The total numbers of contacts made with each species were summed for each plot and expressed as percentages of the totals. Similar percentages obtained from the mapping method were used for comparison, because mapping was probably the most reliable standard available.

The discrepancies between the two methods show clearly the failure of the simple line transect to take account of differences in conspicuousness between species. The relative abundances obtained, which were the object of the method, were thus not valid. The differences between methods were greatest on the closed spruce and pine plots, and least on the open larch, pine, and birch, where the more conspicuous

TABLE 24 - COMPARISONS OF RELATIVE ABUNDANCES DETERMINED BY SIMPLE LINE TRANSECT (T) AND MAPPING (M) METHODS.

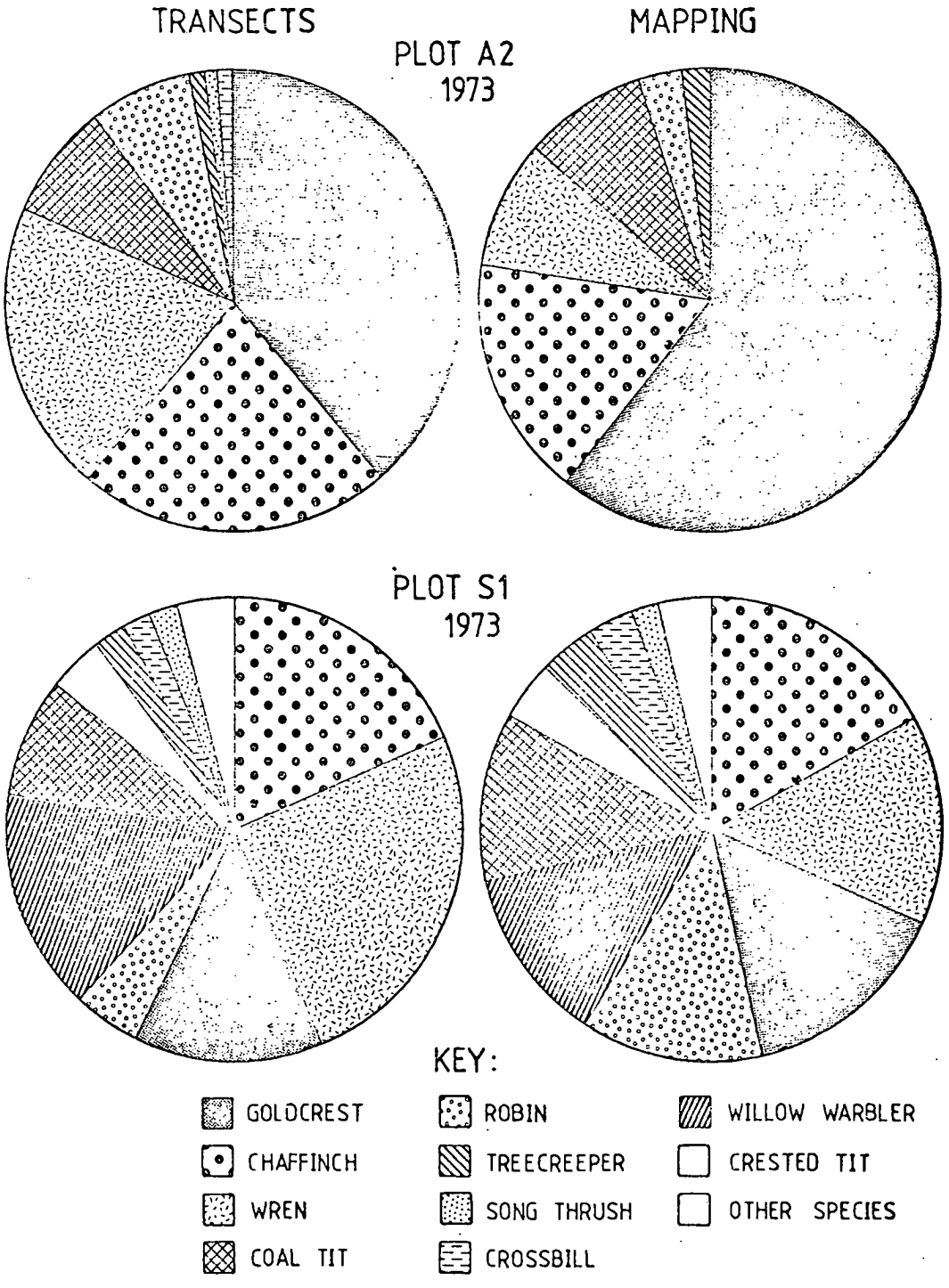
Abundances are expressed as percentages of the totals for all passerine species. See also Figure 20.

Year and plot:	1973 A1		1973 A2		1973 A3		1973 A4	
No. of transects:	7		7		8		8	
Total hours on transects:	13.2		12.6		14.1		14.7	
Total Km. covered on transects:	21.3		20.1		23.1		19.2	
	T	M	T	M	T	M	T	M
Total number of contacts/ territories:	820	38¾	947	55	850	46½	806	25¾
Percentages of:								
Goldcrest	25	39	38	62	39	62	17	22
Chaffinch	27	29	22	17	26	13	22	18
Wren	24	16	20	9	19	13	29	26
Coal Tit	7	6	8	8	9	6	10	11
Robin	5	1	7	3	2	1	9	11
Treecreeper	3	3	1	2	1	2	2	4
Mistle Thrush	2	1	0	0	0	0	1	0
Song Thrush	3	0	1	0	2	0	3	0
Siskin	1	3	0	0	1	1	1	0
Crossbill	0	3	1	0	1	1	0	0
Others	2	0	0	0	1	0	7	8

TABLE 24 (continued)

Year and plot:	1974 A2		1974 A3		1973 S1		1973 S2		1973 S3	
No. of transects:	8		8		3		3		3	
Total hours on transects:	11.6		12.6		5.6		5.7		5.5	
Total Km. covered on transects:	20.0		22.4		8.9		10.5		9.9	
	T	M	T	M	T	M	T	M	T	M
Total number of contacts/territories:	798	50¾	780	56¼	296	33½	278	18¼	333	36¾
Percentages of:										
Goldcrest	32	54	38	58	13	15	23	37	2	8
Chaffinch	21	11	20	15	18	17	36	28	29	27
Wren	23	13	18	13	25	15	10	3	14	11
Coal Tit	6	9	11	7	8	12	13	17	3	3
Robin	11	6	8	4	5	13	8	6	6	8
Willow Warbler	0	0	0	0	15	12	4	0	22	22
Blue Tit	0	0	0	0	0	0	0	0	4	10
Crested Tit	0	0	0	0	4	4	0	3	0	0
Treecreeper	2	3	1	2	2	4	2	6	0	0
Mistle Thrush	1	0	1	0	0	0	0	0	1	0
Song Thrush	0	0	1	1	2	2	3	3	3	3
Redstart	0	0	0	0	1	0	0	0	8	7
Siskin	3	2	1	0	1	2	0	0	0	0
Crossbill	0	2	1	0	2	3	0	0	0	0
Others	1	0	1	0	2	2	0	0	8	1

FIGURE 20 - COMPARISONS OF RELATIVE ABUNDANCE DETERMINED BY SIMPLE LINE TRANSECT AND MAPPING METHODS.



species, Chaffinch and Wren, were the most numerous (Table 24 and Figure 20). Some of the discrepancies were caused when birds off the actual census plots were recorded on transects; for example, Willow Warbler accounted for 4% of transect contacts on plot S2, but the birds were beyond the plot boundary.

Estimates similar to those of Colquhoun (1940a) were made of the conspicuousness of some species (Table 25). Conspicuousness was expressed as the ratio of the percentages of representations on transects and on mapping respectively. The abundances of Goldcrests and of the unobtrusive Treecreeper were under-estimated by 40% on transects, while Chaffinch was over-estimated by the same margin, and Wren, with its penetrating song, by 60%. Only the Coal Tit was represented almost equally by the two methods.

The results showed that the simple line transect was of little value for estimating relative abundance, and gave good information only on the presence or absence of the various species. It did not, of course, give densities.

TABLE 25 - CONSPICUOUSNESS INDICES[1] FOR THE COMMONER SPECIES DERIVED FROM A COMPARISON OF SIMPLE LINE TRANSECTS AND MAPPING CENSUSES IN AE FOREST[2].

Species	Index
Goldcrest	60
Chaffinch	139
Wren	160
Coal Tit	110
Robin	181
Treecreeper	60

[1] Index of conspicuousness = $\frac{\%\text{ representation in transects}}{\%\text{ representation in mapping}} \times 100$.

A value of 100 would represent consistency between the methods; more than 100, over-representation on transects, and less than 100, under-representation on transects.

[2] Data were restricted to Ae Forest, since Spey valley transect samples were small.

3.5 Complex line transects

Emlen's (1971) method of using transects to obtain density estimates was tested by series of transects in 1973-4. All the plots used were also used for mapping censuses (Table 18), so that full comparisons between results could be made.

3.5.1 Method

On each transect, series of routes across the plot were walked for a total of 1.5-2 hours, so that all parts of the plot were sampled at least once on each transect. At all times a definite line was followed, and for each bird detected the following details were noted:

1) Species

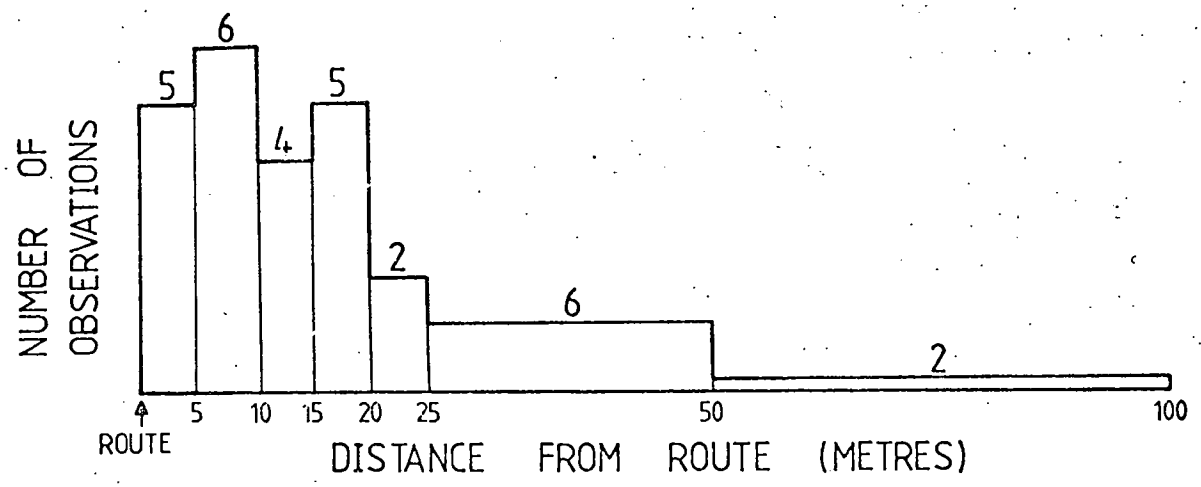
2) Whether singing, calling, seen, or flushed

3) Distance perpendicular to the line being followed, in one of the categories: 0-5, 5-10, 10-15, 15-20, 20-25, 25-50, 50-100, 100+ metres.

Turning points and times were noted, using the grid system marked out for the mapping census, so that the total distance covered could be calculated with the aid of a 1:2000 map. The total time spent and the weather were also recorded. The transects, like the other census visits, were made in the first five hours after sunrise, between late March and mid-June, and were not made in bad weather.

After each transect, histograms were drawn for each species of the number of observations against the distance from the route (Figure 21). From each histogram a plateau width was estimated in which approximately constant numbers of birds were detected. The coefficient of detectability (C.D.) was then calculated. This was the ratio of the number of birds actually observed up to 100 m range to the projected number when the density found on the plateau was extended uniformly to 100 m. Then on this transect, and on

FIGURE 21 - AN EXPLANATORY EXAMPLE OF THE COMPLEX TRANSECT METHOD.
See text.



Route length = 2000 metres

Plateau width = 20 metres

20 observations on 'plateau' projects to 100 in 100 metre strip

There were 30 actual observations up to 100 metres, therefore

coefficient of detectability (C.D.) = $\frac{30}{100} = 0.3$

Area covered = 2000 x 200 m^2 = 0.4 km^2

Therefore the estimated density = $\frac{\text{number observed}}{\text{C.D.}} \times \frac{1}{\text{area in km}^2}$ pairs/km^2

$= \frac{30}{0.3} \times \frac{100}{40} = 250$ pairs/km^2.

subsequent transects when this C.D. was appliable, the number of pairs observed in the 200 m wide strip was divided by the C.D. and by the area (km^2) covered (i.e. 0.2 X the transect length in km) to give the number of pairs per km^2, corrected for inconspicuousness.

My method differed a little from Emlen (1971) in the estimation of the number of pairs observed. He took song and non-song registrations separately, and counted one pair for each singing bird, and a half pair for the others. He then took as his density value the greater of the two densities obtained. I counted one pair for a singing bird, and added a half-pair for other observations, on the assumption that they were equally likely to be of either sex, and then used a C.D. value based on all observations. This procedure maximised the sample sizes. I also calculated a separate set of densities from song observations alone, for which separate song-only C.D. values were used.

It might have been more realistic to take for example 0.8 pairs for each non-song observation, to take account of the greater conspicuousness of males than of females during the breeding season; when this was tried it increased the uncorrected densities, lowered the incompleteness factors, and made little change to the variability of corrected results. Emlen's approach would have been likely to increase inconsistency in the results, since the song density would have been used in some cases and the non-song density in others. In the transects made here, the song density was always greater for all species (usually by at least a factor of two) than the non-song density when taken over a complete season. The song density was also the greater in almost all individual transects, with a small number of exceptions when few birds were singing.

3.5.2 Results

C.D. values and densities were calculated for each species on each transect when at least ten birds had been counted within the 100 m zone, and densities could be obtained for scarcer species by using the C.D. value calculated over a series of transects. For each species and plot, the observations on a total of seven or eight transects in the season were amalgamated, and C.D. values and densities were calculated again as above (Table 26). These densities were divided into the corresponding mapping census densities for the same species and plots to give the incompleteness factors (I.F.) (Table 26). Both densities from all observations and those from singing birds alone were treated. Finally each observed density on each individual transect was multiplied by the appropriate I.F. to obtain a corrected density (Table 28).

The incompleteness factors corrected the densities obtained from complex transects for that proportion of birds which failed to be detected. I thought that the mapping census was the most reliable standard available from which to calculate the I.F. Although Emlen (1971) did not have much faith in the mapping method as a baseline, he had to use it to calculate his I.F. values for lack of any method which he thought superior.

Unlike the simple line transects, the current method took account of differences in conspicuousness. The parameters C.D. (coefficient of detectability) and I.F. (incompleteness factor) were two parts of the conspicuousness of the species. They were interpreted biologically as follows: the C.D. when multiplied by the strip width (100 metres) was approximately the same as the average range over which the bird was detectable. For example, Goldcrest on plot A1, 1973, gave C.D. = 0.315, and so was on average detectable up to 31.5 metres away.

TABLE 26 - TRANSECT DENSITIES OF THE COMMONER SPECIES OBTAINED FROM THE COMBINATION OF TRANSECTS MADE OVER THE SEASON, INCOMPLETENESS FACTORS, AND COEFFICIENTS OF DETECTABILITY (see Section 3.5.1 for explanation of terms).

Results based

(a) on all observations, taking one pair for a singing bird and 0.5 pairs for other observations

(b) on singing birds only, taking one pair for a singing bird

	1973				1974		1973		
	A1	A2	A3	A4	A2	A3	S1	S2	S3
Goldcrest									
mapping density	136	372	283	99	296	317	57	57	34
transect dens. (a)	107	220	168	79	158	162	44	64	6
I.F.	1.27	1.69	1.68	1.25	1.87	1.96	1.30	0.89	-
C.D.	.315	.287	.293	.320	.303	.315	.330	.332	-
Transect dens. (b)	61	123	87	40	108	112	31	29	-
I.F.	2.23	3.02	3.25	2.48	2.74	2.83	1.84	1.97	-
C.D.	.358	.311	.333	.400	.316	.344	.255	.433	-
Chaffinch									
mapping density	102	101	59	82	60	83	66	43	114
transect dens. (a)	74	48	42	55	53	35	33	33	78
I.F.	1.38	2.10	1.40	1.49	1.13	2.37	2.00	1.30	1.46
C.D.	.478	.667	.815	.592	.522	.599	.592	.789	.425
transect dens. (b)	43	32	33	38	39	24	22	19	36
I.F.	2.37	3.16	1.79	2.16	1.54	3.46	3.00	2.26	3.17
C.D.	.573	.746	.890	.681	.568	.694	.625	.975	.639
Wren									
mapping density	57	52	59	116	71	73	57	4	45
transect dens. (a)	44	42	47	72	54	35	34	6	22
I.F.	1.30	1.24	1.26	1.61	1.31	2.09	1.68	-	2.05
C.D.	.857	.852	.630	.717	.618	.722	.867	1.00	.750

TABLE 26 (continued)

	1973				1974		1973		
	A1	A2	A3	A4	A2	A3	S1	S2	S3
Wren (continued)									
transect dens. (b)	39	36	42	69	36	33	34	6	20
I.F.	1.46	1.44	1.40	1.68	1.97	2.21	1.68	-	2.25
C.D.	.910	.925	.667	.723	.896	.733	.867	1.00	.775
Coal Tit*									
Mapping density	20	49	29	47	49	41	46	26	40
Transect dens. (a)	13	22	13	29	15	33	18	15	8
I.F.	1.54	2.23	2.23	1.62	3.27	1.24	2.56	1.73	5.00
C.D.	.727	.755	.750	.546	.556	.428	.364	.614	.464
Transect dens. (b)	11	17	10	18	11	16	-	5	-
I.F.	1.82	2.88	2.90	2.61	4.45	2.56	-	-	-
C.D.	.761	.841	.826	.700	.614	.667	-	1.00	-
Robin									
Mapping density	5	16	5	47	35	20	49	9	34
Transect dens. (a)	9	16	3	22	22	15	8	9	16
I.F.	-	1.00	-	2.14	1.59	1.33	6.13	-	2.13
C.D.	.789	.794	-	.750	.716	.603	.929	.833	.429
Transect dens. (b)	8	14	-	22	22	13	8	9	10
I.F.	-	1.14	-	2.14	1.59	1.54	6.13	-	3.40
C.D.	-	.875	-	.750	.716	.650	.929	.833	.600

Willow Warbler	1973 S1	1973 S3	Redstart	1973 S3
Mapping density	46	91		31
Transect dens. (a)	39	85		28
I.F.	1.18	1.07		1.11
C.D.	.795	.587		.611
Transect dens. (b)	39	73		25
I.F.	1.18	1.25		1.24
C.D.	.795	.663		.656

* Blue Tit on plot S3

The ratio 1:I.F. was the ratio of individuals close to the route which were detected. The I.F. should not fall below unity, but did so in one case (Goldcrest on plot S2), possibly because of an under-estimate in the mapping census density.

The reliability of the method as applied by Emlen (1971) could be examined. From Table 26, it was possible to find the error inherent in the assumption that the C.D. and I.F. were constant for a particular habitat and time of year. Emlen claimed that these parameters were accurate within rather broad limits of acceptability, and applicable over a considerable range of habitats and seasons. The five spruce plantation transect series were used to test this claim, since all were of the same habitat type, and means and standard deviations of the parameters for the three commonest species were calculated (Table 27). To apply the line transect method to obtain densities in pairs/ km^2, the transect count was standardised to a length of 5 km, divided by the C.D., and multiplied by the I.F. for the habitat and time of year, so it was the variability of the factor I.F./C.D. which was considered. The means, standard deviations, and 95% confidence limits of this factor over the five spruce plots were also calculated.

For the three commonest species, the confidence limits of I.F./ C.D. were between $\pm$20% and $\pm$39% of the mean for the five spruce plantations (Table 27); whether these were within the limits of acceptability, and so a single value of I.F./C.D. could be used for all spruce plantations, would depend on the requirements of the census. The confidence limits of the I.F. alone changed by no more than 4% of the mean if the C.D. was calculated separately for each plot.

So far, only the combined results of several transects have been considered. Densities were calculated for each individual transect, and their consistency between transects of the same plot was examined

TABLE 27 - VARIATION OVER FIVE TRANSECT SERIES IN SPRUCE PLANTATIONS IN THE FACTORS I.F. AND C.D. AND THEIR QUOTIENT, AND 95% CONFIDENCE LIMITS OF THE MEAN OF THE QUOTIENT, FOR THE THREE COMMONEST SPECIES. For derivation, see text.

Separate calculations were made for (a) combined, and (b) song only data, as in Table 26.

	Goldcrest	Chaffinch	Wren
(a)			
Mean I.F. $\pm$ s.d.	1.69$\pm$0.27	1.68$\pm$0.53	1.44$\pm$0.36
Mean C.D. $\pm$ s.d.	.303$\pm$.013	.616$\pm$.133	.736$\pm$.116
Mean I.F./C.D. $\pm$ s.d.	5.61$\pm$0.90	2.77$\pm$0.87	2.00$\pm$0.58
Confidence limits of IF/CD	4.49-6.73	1.69-3.85	1.28-2.72
(b)			
Mean I.F. $\pm$ s.d.	2.81$\pm$0.38	2.46$\pm$0.84	1.70$\pm$0.37
Mean C.D. $\pm$ s.d.	.332$\pm$.019	.694$\pm$.134	.826$\pm$.118
Mean I.F./C.D. $\pm$ s.d.	8.52$\pm$1.44	3.62$\pm$1.22	2.09$\pm$0.59
Confidence limits of IF/CD	6.73-10.31	2.11-5.13	1.36-2.82

(Table 28). There were too few transects in the Spey valley plots for such an evaluation to be made there, so discussion is restricted to the Ae Forest transects. In order to maximise sample sizes, only results based on both song and other observations, combined as described earlier, were used. Marked fluctuations in density estimates based on individual transects occurred. The 95% confidence limits of the mean transect density were around ±33% of the mean for the Goldcrest, up to ±40% for Wren, around ±50% for Chaffinch, and about ±60% for the scarcer Coal Tit.

The variation in the individual transect results obtained on different days throughout the period April to June could be ascribed to a number of sources:

1) Variation in the proportion of birds active and likely to be detected at different stages of the breeding cycle.

2) Variation in the intensity of the birds' activity from day to day.

3) Observer error, particularly due to difficulties in estimating distances, heightened in poor weather.

4) Smallness of the individual samples on which the transect results were based.

The consequence of (1) was a fluctuating value of the I.F. during the season, and no allowance could be made for this without a detailed study of song activity, such as that by Slagsvold (1973a) on the Song Thrush. (2) and (3) resulted in variations in the observed C.D. values, while (4) affected both the individual I.F. and the C.D. values. The transect densities were analysed for the effect of varying values of C.D., and significant negative correlations were found between transect density and C.D. on all six series of transects for Chaffinch, and on three out of six for Goldcrest and Wren. This

TABLE 28 - RANGE, MEAN, STANDARD DEVIATION AND 95% CONFIDENCE LIMITS OF THE MEAN OF CORRECTED DENSITIES FROM INDIVIDUAL TRANSECT RESULTS.

Densities based on the combination of all types of observations.

Year:	1973				1974	
Plot:	A1	A2	A3	A4	A2	A3
Number of transects:	7	7	8	8	8	8
Goldcrest						
Minimum density	86	218	170	35	146	178
Maximum density	207	630	417	114	533	525
Mean ± s.d.	150±41	387±172	294±84	100±38	294±122	310±116
Confidence limits	109-191	215-559	219-369	66-134	185-403	206-414
Chaffinch						
Minimum density	51	27	31	13	31	45
Maximum density	283	185	140	143	95	199
Mean ± s.d.	105±81	103±53	65±36	79±45	57±20	98±53
Confidence limits	24-186	50-156	33-97	39-119	39-75	51-145
Wren						
Minimum density	43	40	21	79	30	33
Maximum density	127	102	95	190	79	132
Mean ± s.d.	69±30	60±24	54±23	130±35	56±18	77±31
Confidence limits	39-99	36-84	33-75	99-161	40-72	49-105
Coal Tit						
Minimum density		27	13	10	23	14
Maximum density		91	85	94	118	87
Mean ± s.d.		54±25	36±27	42±31	52±33	41±29
Confidence limits		29-79	12-60	14-70	23-81	15-67

suggested that the C.D. values should not have been calculated separately for each transect, since it was liable to the causes of variation given in (2) and (3) above. Accordingly, the transect densities were re-calculated (Table 29), using for C.D. the values (given in Table 26) obtained for the species from the complete series of transects, seven or eight in all, on the plot concerned.

The 95% confidence limits were reduced to ±30% of the mean for Goldcrest, and Wren, ±30-40% for Chaffinch, and around ±55% for Coal Tit. There were two cases (marked *, Table 29), where the error increased compared with the original calculation (Table 28): Coal Tit on plot A4, where the individual C.D. could only be calculated for a few of the transects because samples were small, and was then lower than the overall C.D. value; and Goldcrest on plot A4, where there was no correlation between transect density and observed C.D. This plot was unusual in that Goldcrests were concentrated in clumps of spruce within the larches, so that the transect density varied with the proportion of the transect route which passed close to the spruce clumps.

To summarise, the transect method, if reliable, might have been useful to determine densities quickly. However in practice the results obtained were too inconsistent to give valid densities even when transects were replicated to such an extent that they were as time consuming as the mapping census method.

TABLE 29 - AS TABLE 28, BUT WITH INDIVIDUAL TRANSECT DENSITIES CALCULATED USING THE C.D. VALUE FOR EACH COMPLETE SERIES OF TRANSECTS.

Year:	1973				1974	
Plot:	A1	A2	A3	A4	A2	A3
Number of transects:	7	7	8	8	8	8
Goldcrest						
Minimum density	118	251	153	49	209	190
Maximum density	186	592	358	201	471	471
Mean ± s.d.	137±24	374±123	286±80	102±49	295±89	310±100
Confidence limits	113-161	251-497	214-358	58-146*	215-375	221-399
Chaffinch						
Minimum density	58	27	30	13	31	45
Maximum density	190	161	88	126	80	155
Mean ± s.d.	105±46	105±42	66±23	83±36	59±16	88±35
Confidence limits	59-151	63-147	45-87	51-114	45-73	57-119
Wren						
Minimum density	42	26	22	80	49	34
Maximum density	83	61	72	141	103	109
Mean ± s.d.	58±15	47±15	55±17	117±25	72±20	73±24
Confidence limits	43-73	32-62	40-70	95-139	54-90	52-94
Coal Tit						
Minimum density		26	13	10	23	14
Maximum density		95	61	119	118	89
Mean ± s.d.		50±23	30±19	48±42	52±33	41±25
Confidence limits		27-73	13-47	10-86*	23-81	19-63

* Confidence limits wider than in Table 28. See text.

3.6 Fixed-time counts

3.6.1 Method

In 1975 a series of fixed-time counts was made. Since these censuses could be used for restricted areas, the eight census points were all chosen at Sparrowhawk nest territories within Ae Forest where growth rates had been measured in 1973-4. Three sites were in each of the remote and edge areas of the forest (p.50), and two in the central area. Direct estimates of prey abundance in these territories were attempted by this means.

On each visit observations were made from a fixed point in ten consecutive five-minute periods. Each individual bird heard or seen in each period was counted. In order to facilitate the separation and counting of individual birds, records were divided according to their directions by four points into quadrants. On each day devoted to these counts, four sites were visited in the first five hours after sunrise, and the order of visits was reversed on alternate occasions to avoid any bias due to decreased activity in the later hours. Four visits were made to each site between early April and mid-June.

Numbers of observations of each species were totalled over the ten five-minute periods and over the four visits. Two of the sites coincided with mapping census plots, so that estimates of species composition could be compared between the two methods.

3.6.2 Results

Fixed-time counts, like simple line transects, took no account of differences in conspicuousness between species (Table 30). Of the two sites at which a direct comparison between the mapping and fixed time methods was possible, significantly different distributions were found between the methods at one. The sites were Gubhill, which lay on plot A2, and Blue Cairn, which was near to plot A5 and in similar

TABLE 30 - FIXED-TIME COUNT RESULTS.

Relative abundances of each species expressed as percentages of the totals.

	Forest Area:								
	Edge			Central		Remote			
	Site:								
Species	Wood Hill	Graveyard	Kirkland Burn	Gubhill	Cat Cleugh	Sharp Bend	Mitchell-slacks	Blue Cairn	Total
Goldcrest	15	19	23	20	22	26	20	22	21
Chaffinch	19	43	31	24	27	19	16	21	25
Wren	21	4	11	30	23	24	28	9	20
Coal Tit	10	5	8	4	5	6	5	10	7
Robin	11	10	6	12	11	10	11	15	11
Willow Warbler	4	-	0	0	9	-	11	-	3
Blue Tit	6	-	-	-	-	-	-	-	1
Treecreeper	1	-	-	3	-	0	-	-	1
Mistle Thrush	2	-	6	-	-	1	3	4	2
Song Thrush	5	9	9	2	1	4	0	5	4
Blackbird	-	3	2	-	-	1	1	-	1
Chiffchaff	-	4	2	-	-	-	-	-	1
Dunnock	1	1	-	-	-	-	-	2	0
Siskin	2	0	1	3	-	4	1	11	2
Redpoll	-	-	-	0	-	1	0	-	0
Bullfinch	1	0	0	2	0	2	-	-	1
Crossbill	-	-	1	0	-	1	2	2	1
Others[1]	3	0	-	-	0	-	2	-	1
Total number of records:	379	284	296	322	269	304	335	185	2374

[1] Species which occurred at only one site: Long-tailed Tit, Jay, Grey Wagtail, Cuckoo.

0 denotes species which were recorded, but formed less than 0.5% of observations.

habitat. At the former site, a χ^2 test of consistency between the two methods for the five major bird species showed a significant difference ($\chi^2_3 = 21.2$, $P < .01$), while at the latter the difference was not significant ($\chi^2_3 = 4.3$). In both comparisons, as with the simple line transects (section 3.4), the Goldcrest was under-recorded on fixed time counts, while the Chaffinch and Wren were over-recorded.

A further problem with the fixed time censuses was that the range of audibility varied from species to species, and also with density. Thus birds with loud songs, such as Song Thrush, were recorded from a radius of at least 200 m, while Goldcrests had a range little over 50 m. Where a species was numerous, individuals in the range 50-100 m were probably not recorded when several others were within 50 m, but they were heard when there were no individuals of that species close by, with the result that the radius of observation decreased as density increased. This would tend to make the number of observations more uniform between sites than they should properly have been. In view of these limitations, which also applied to comparisons between sites for individual species, the method as it was applied was of little value when compared with the mapping method.

Although these censuses were made at Sparrowhawk nest sites, five of which were occupied during the census period, the predator was unlikely to have influenced the results or caused a decline in numbers during the season because the male seldom hunts near the nest and the female does not hunt during the period when the counts were made.

3.7 Discussion of the census methods

Several problems inherent in the assessment of woodland song-bird populations were common to all methods. Some of these problems have been mentioned earlier, but can be brought together here:

1) The inconspicuousness of all species in a dense woodland habitat with large areas of continuous canopy. Almost all birds must be located by sound alone, which makes distance hard to estimate precisely, although species could be distinguished easily.

2) The differences in conspicuousness between species caused by the penetrability of their songs and calls, frequency of singing, colouration, behaviour, and response to neighbours.

3) The day to day variations in birds' activities, only partly caused by weather, and longer term variations according to stage of breeding.

4) The presence of transient and non-territorial birds, which may be attempting to take up a territory, singing in the process.

5) The chance disappearance of territory holders during the breeding season, for example due to predation by Sparrowhawks.

The complex line transect method took account of differences in conspicuousness under (2) above, but longer term changes, (3) above, caused sizeable errors in density estimates. The difficulty in the estimation of distances of bird sounds would have given rise to errors in the C.D. values, but these were minimised by using the more broadly-based C.D. values. Emlen (1971) recommended that transects be 10 miles (16 km) in length, or at least not less than 5 miles (8 km), in order to be reliable. Due to limitations in time and the sizes of the plots, the transects used in this study were only about 3 km, so that, to have followed the recommendations, they should have been up to five times as long. From the sources of variation given for

the transect method (p.131), only variations due to the smallness of the sample size would have been reduced by an increase in transect length. At most the confidence intervals (Table 29), which were themselves derived from means of 7-8 transects, could have been halved for similar series of 16 km transects. However the errors due to variations between plots in the "constant factors" (Table 27) would have remained, and the two sets of errors would have been combined if transect densities from each plot had used common estimates of I.F./C.D. Thus the complex transect method was effective in terms of area covered in unit time (over 30 ha per hour), but its results were unreliable, except as an approximate guide. The variability of individual transect densities was higher again than that of series of transects (Table 29).

In order to eliminate the variability in the factor I.F., mapping censuses were required for each plot, while series of several transects rather than individual transects, even of 16 km, were necessary in order to minimise the effects of daily chance fluctuations. Either of these operations defeated the object in using the transect method extensively, that is efficiency in terms of time required per unit area censused.

The simple line transects were useful only for listing the species present on a plot, but failure to consider differences in conspicuousness between species rendered quantitative results which were in poor agreement with other methods. Yapp (1974) asked why so few workers had used this method in Britain; perhaps it is because of this basic failure.

Fixed-time counts were also useful only for listing species in a particular area, because differences in conspicuousness between species caused each to have a different radius of observation. The radius

also decreased as density of a species increased, since more distant songs and calls were swamped by nearer ones. Any attempt to improve the fixed-time method by estimating the distance of each bird from the observation point and then finding a "plateau" radius similar to the plateau in the complex transect method (p.123), or by restricting observations to those within a certain radius, would have been subject to the same problems as were encountered in the application of the complex transect method.

The mapping census was the best suited to overcome the problems mentioned above, but had its own particular defects. It was less sensitive than the transects to errors in the location of observations, provided these were not so great as to place a bird where it would be ascribed to a new, false, territory. A small proportion of territories was likely to be missed completely (Table 21), but the error from this source would not have been expected to exceed 5% provided that ten visits were made to each plot. There was a subjective element in the interpretation of the species maps which, despite the use of standard rules, could not be eliminated. Other people could interpret the maps independently, but without the field experience their judgements would have been less reliable than the observer's. Since only one set of densities resulted from a whole season's work on each plot, no comparisons for reliability similar to those for the transect results could be made. The method was time consuming, and required on average two hours for every hectare covered, disregarding the additional time required to reach the plot on ten visits, and an average of 15 hours to mark out a 50 m grid.

The problem of transient birds may be more widespread than is generally realised. Pielowski & Wasilewski (1972) compared settled and transient birds using mapping and netting techniques in a Polish

forest, and found a high proportion of transients. Removal experiments, for example by Stewart & Aldrich (1951), showed that there was a ready supply of birds in search of a territory, and Bulmer & Perrins (1973) estimated that 34% of first-year male Great Tits could not breed for lack of mates. However a transient bird or a series of transients would have been unlikely to persist in the same locality long enough to have been registered on three census visits, and so would not have qualified as an additional territory. If recorded on a transect, a transient would not have been distinguished, and so would have contributed to over-estimation of density.

Predation of birds on the census plots was unlikely to have been important since, with the evidence given above, some of the birds lost should have been replaced over at least half the census period by other birds seeking territories.

Despite its defects, the mapping method countered all the possible sources of error listed earlier. Although observer bias may have affected the absolute densities found, comparisons between plots which are made here are valid, since all plots were censused and interpreted by the same person, so that consistency was maximal. The greater reliability of the mapping method by comparison with the complex transects can be explained quite simply. Information about the total bird populations and distributions was gathered on each visit to each plot using the mapping method, and at the end of the season several pictures of the distributions were built up. These were interpreted to give the density figures. By contrast, each transect was a complete entity, and results were based either completely on observations made on a single occasion, or on a series of occasions which became as time consuming as the mapping census. When single transects were used, the results were subject to several sources of

error, particularly day to day variations in activity, and were too inconsistent to be used in comparisons, while when series of transects were made, the results were still less reliable than those from the mapping method. Mapping and complex transect methods were each much more useful than simple transects and fixed-time censuses, since these did not allow at all for differences in conspicuousness between species.

3.8 The song-bird communities of different woodland types

The discussion in this and the following sections is based on the results of the mapping census, since these were considered to be the most reliable of those obtained. Parts of sub-sections 6, 7, and 10 are to be published by Newton & Moss (in press). Reference should be made to Tables 19 and 31 and Figure 14 throughout.

Several larger non-passerine birds such as Woodpigeon and Capercaillie were recorded on the census plots, but could not be censused reliably because they were not territorial. The census results are restricted to territorial species.

The annual differences in the results for the plots censused more than once showed that there were no drastic changes in densities from year to year, except on plot A1 where the habitat changed due to a wind-blow in January 1974. The two winters of 1973/4 and 1974/5 were relatively mild, so that populations remained stable from year to year.

3.8.1 Spruce plantation plots

Spruce plots provided the largest category of census results, with a total of 11 censuses on 6 plots, 4 in Ae Forest and 2 in Greskine Forest, Dumfries-shire. Total densities (Table 31) ranged from 351 to 598 pairs/km^2, and were lowest in the plot with the oldest trees and most open canopy (A1). Diversities both of bird species and of foliage structure were the lowest of any found. Among the spruce plots, diversity of bird species was highest on the most mature and open plot (A1).

On all spruce plots Goldcrest was the most numerous species, making up 32-70% of the total population; it comprised over 50% on three plots. The next most common species were Chaffinch and Wren, while Coal Tit, Robin, and Siskin on one census were the only other

TABLE 31 - MAPPING CENSUS RESULTS: densities of song-bird species on each plot in pairs per km^2. Numbers of species holding territories, and bird species diversities[1].

For descriptions of plots see Table 19 and Figure 14.

(1) Ae Forest

Species	1973 A1	1974 A1	1973 A2	1974 A2	1975 A2	1973 A3	1974 A3	1975 A3	1973 A4	1974 A4	1975 A5
Goldcrest	136	140	372	296	261	283	317	244	99	125	172
Chaffinch	102	86	101	60	73	59	83	61	82	73	96
Wren	57	100	52	71	73	59	73	66	116	121	25
Coal Tit	20	48	46	49	43	29	41	59	47	65	41
Robin	5	45	16	35	30	5	20	24	47	30	53
Willow Warbler									17		
Jay										9	
Long-tailed Tit									17		
Treecreeper	9		11	19	5	10	10	10	17	9	
Mistle Thrush	5	9								9	
Song Thrush							5			9	
Dunnock											9
Siskin	9	5		11	11	5					5
Bullfinch					5						
Crossbill	9	9		11		5					9
Total	351	441	598	552	503	454	549	498	444	448	411
Number of species	9	8	6	8	8	8	7	8	8	9	8
Diversity[1]	1.582	1.699	1.174	1.497	1.462	1.230	1.299	1.563	1.854	1.771	1.591

[1] Diversity = $-\sum p_i \log_e p_i$ where p_i = proportion of total due to ith species.

TABLE 31 (continued)

(2) Greskine Forest & Annan valley pine woods

Species	1973 G1	1973 G2	1975 T	1975 W
Goldcrest	247	417	36	34
Chaffinch	125	145	30	88
Wren	80		75	92
Coal Tit	28	21	34	57
Robin	23	14	20	29
Treecreeper			16	13
Willow Warbler				23
Blackbird	6			
Dunnock				4
Siskin	6			
Crossbill	6			
Total	520	597	208	340
Number of species	8	4	6	8
Diversity	1.428	.797	1.662	1.803

TABLE 31 (continued)

(3) Annan valley mixed plots

Species	1974 H	1975 H	1974 K	1975 K	1974 D_1	1975 D_1	1974 D_2	1975 D_2
Goldcrest	21	35	39	58	70	47		
Chaffinch	124	167	45	74	302	256	250	139
Wren	146	173	71	74	186	302	83	97
Coal Tit	8	17	45	45	70	93		
Robin	92	122	79	63	140	209	28	28
Willow Warbler	292	283	105	105	279	209	250	222
Great Spotted Woodpecker			5		12			
Jay			5	5				
Great Tit		4		5	70	93		
Blue Tit	25	25	16	11	186	116	28	
Willow Tit	29	25		11		23		
Long-tailed Tit	4	13	11	11	23	23		
Treecreeper	8		5	16	47	93		
Mistle Thrush	4				23	23		
Song Thrush	17	13	5	11	23	47	14	
Blackbird	17	13	16	16	47	70	56	28
Redstart					23	23		
Sedge Warbler							14	28
Blackcap		8						
Garden Warbler	8	8	5					28
Whitethroat							28	28
Spotted Flycatcher	4				23	23		
Dunnock	4			5			28	28
Tree Pipit				5				
Starling					70	70		
Greenfinch						23		
Redpoll	8	17						
Crossbill			11					
Yellowhammer				5			56	56
Reed Bunting	8	8					56	56
Total	825	935	463	518	1593	1744	889	736
Number of species	18	16	15	17	17	18	12	11
Diversity	2.022	2.038	2.245	2.353	2.434	2.540	2.019	2.075

TABLE 31 (continued)

(4) Spey valley

Species	1973 S1	1974 S1	1973 S3	1974 S3	1973 S2	1974 S2	1975 S2	1975 S4
Goldcrest	57	83	34	11	57	60	34	22
Chaffinch	66	95	114	159	43	66	74	26
Wren	57	63	45	51	4	9	4	44
Coal Tit	46	52	11	34	26	43	38	35
Robin	49	43	34	28	9	4	4	22
Willow Warbler	46	55	91	114				
Blue Tit			40	40				
Crested Tit	17	11			4	4	4	4
Treecreeper	17	11			9	4		
Mistle Thrush						4		
Song Thrush	6		11	6	4			
Redstart			31	6				
Dunnock	6							
Starling			6					
Siskin	6	46				17	13	
Bullfinch		11				4		
Crossbill	11							
Reed Bunting				6				
Total	385	471	418	455	155	215	172	151
Number of species	12	10	10	10	8	10	7	6
Diversity	2.210	2.109	2.010	1.796	1.633	1.757	1.485	1.646

species to exceed 5% of the total populations. A total of 13 species was found in spruce.

3.8.2 Larch plantation

The only larch plot censused (A4) did not consist purely of Japanese larch, but contained small areas of spruce and pine. These increased the diversity of its structure, and certain species, particularly Goldcrest and Chaffinch, were found mainly in the evergreen trees. Probably, therefore, pure larch stands would support very small bird populations, but no blocks of larch were large enough to test this.

3.8.3 Annan valley pine plantations

Total densities in the two pine plantations in Dumfries-shire (208 and 340 pairs/km^2) were lower than on the spruce plots, although bird and foliage diversities were similar. Of the two plots, W had the greater density, but was situated at the edge of a plantation bounded on two sides by fields, and so probably enjoyed a considerable edge effect (Odum 1971), while plot T was completely surrounded by similar trees. Only 8 species were recorded in the single year on these plots.

3.8.4 Semi-natural birch/pine

The two areas censused held substantially different total densities, with numbers on plot H (over 800 pairs/km^2) twice those on plot K. Completely open parts of the plots were excluded in the calculation of density. Plot K had the more diverse height structure, and correspondingly higher bird species diversity. However plot H supported the greater total bird density, perhaps because it contained a greater proportion of relatively mature birch woodland, and the thicker scrub (60% cover compared with 40% on plot K) was more dominated by birch on H and by pine on K.

Willow Warbler was the dominant species on both plots, but was virtually absent from the spruce forest, while the reverse held for

Goldcrest. Almost twice as many species (24) held territories on these plots as in the spruce plantations.

3.8.5 Mixed woodland

The highest total density (over 1600 pairs/km^2) was found in the mature mixed woodland plot (D1). This plot also supported the most diverse bird population, although it was not the most diverse in vegetation height structure (at least with the subdivision into height classes used here). The plot thus provided ecological niches for several species so that, although no single species was as numerous as the Goldcrest at its densest in some of the spruce plantations, several species reached 100 pairs/km^2. Those species such as Chaffinch and Wren which were common in both habitats were twice as numerous on D1 as on spruce plots. The small size of the wood (4.3 ha) would also have been likely to contribute to the greater bird density through enhanced edge effect (Odum 1971).

The riverside scrub (plot D2) also held high bird densities, although since there was no canopy above 12 m, these densities were much lower than those in the adjoining woodland (D1). 25 species were mapped on the whole plot D1 + D2.

3.8.6 Spey valley pine

The total densities on the planted plots were less than half as great as those on the semi-natural plot. The diversities on bird species and foliage height were also lower on the plantations (with uniform canopies and little undergrowth) than on the semi-natural plot, which had thick understorey and ground layers. Of the six common species on semi-natural pine (plot S1), the Wren and Robin were scarce in the adjacent plantation (S2), where Willow Warbler was absent altogether. 14 species held territories in the Spey valley pines, of which all but one (Mistle Thrush) were found on S1.

3.8.7 Spey valley birch

The birch plot (S3) was less diversely structured than the semi-natural pine plot (S1) because the trees were less tall, and the understorey was reduced by sheep grazing. Consequently the bird population was less diverse than on S1. Results from censuses elsewhere (von Haartman 1971) supported the suggestion that a birch wood equivalent in structure to S1 might have supported a total bird density about 50% greater than that on the pine; in this case the two plots held similar densities.

The main birch wood species, Chaffinch and Willow Warbler, were more numerous than in pine, while other differences typical of the woodland type occurred, such as the substitution of Blue Tit for Coal Tit in the birch.

3.8.8 Comparison between Annan and Spey valleys

One of the major aims of the census work was to compare bird densities between the two Sparrowhawk study areas. It proved difficult to find comparable woods in the two regions, since spruce predominates in Dumfries, and pine in Inverness. The only plots strictly comparable in type between the two areas were the pine plantations (plots T, W, S2, S4). Of these, all but one had similar total bird densities, and the exception (plot W in Dumfries) was at the corner of a plantation bounded by fields. There was thus little difference between similar woodlands in the two areas.

However if the predominant plantation types in the two regions are compared, that is Annan valley spruce against Spey valley pine (plots A2, A3, G1, S2, S4), total densities in the southern area were two to three times those in the northern one. Further, a comparison of the best woods censused in each of the two areas (D1 with S1 and S3) revealed total densities in the best Annan valley wood three to

four times the best Spey valley densities. It is unlikely that any better woods than the ones censused exist in either area. When the composition of the woodlands of the two study areas was considered, the evidence gained from census results on selected plots suggested that overall bird densities were higher by a factor of at least two in Annan valley woodland than in those of the Spey valley.

3.8.9 Discussion: diversity

As mentioned earlier (p.101), the diversities of bird species and of foliage heights were highly correlated for several choices of height ranges, and the highest correlation ($r = 0.932$) was obtained using the ranges 0-0.6 m, 0.6-6.0 m, 6-15 m, >15 m (Figure 22). When a plot was censused in more than one year, the mean of the annual bird species diversities was used for that plot. Plot A3 was separated into the Norway Spruce (A3N) and Sitka Spruce (A3S) areas because they differed in both bird and foliage diversities.

The correlation observed here is the first European confirmation known to me of the discovery by MacArthur & MacArthur (1961) in temperate North America that bird species diversity was dependent on the diversity of the foliage heights. Later results provided confirmation from the American tropics (MacArthur et al 1966) and from temperate Australia (Recher 1969), all of which fitted the original regression line published by MacArthur & MacArthur (1961). The results presented here do not fit the same line, probably because vegetation profiles were measured differently here.

The correlation (Figure 22) indicates that when another layer is added to the vegetation, the number of ecological niches available to the bird community increases, and the diversity of bird species increases accordingly. This can be seen even within the spruce plantation plots: the foliage of two of them (A3N and G2) was virtually

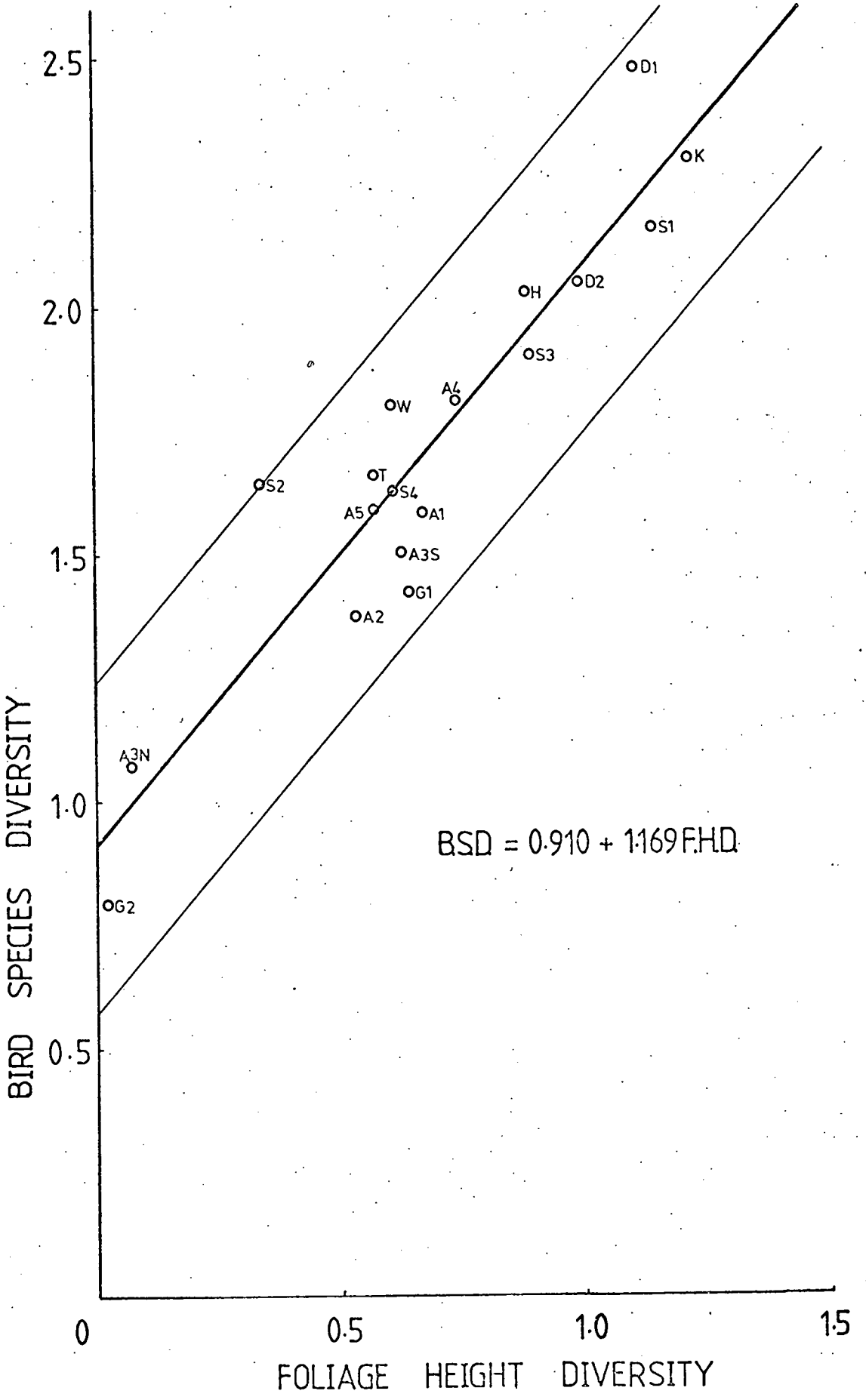


FIGURE 22 - THE RELATIONSHIP BETWEEN BIRD SPECIES DIVERSITY AND FOLIAGE HEIGHT DIVERSITY.

Each point is marked with the plot identification letters. The fine lines show 95% confidence limits for the bird species diversity, given the foliage height diversity.

confined to a single layer (6-15 m), but the other spruce plots possessed two layers, and correspondingly more diverse bird populations (Figure 22). The foliage height diversities of the multi-structured plots K, S1, and D1 were equivalent to more than three equal vegetation layers, and their bird species diversities were correspondingly the highest found.

When the brashings left on the ground in the spruce plantation plots were included with the foliage measurements, the correlation between bird species diversity and foliage height diversity was reduced from 0.932 to 0.860. It would appear from this reduction in the accuracy of the regression that brash was not used by the birds as a substitute for a true ground layer on the spruce plots (except by Wrens, see p.157), and so it was correctly excluded from the earlier calculations. Dead branches were similarly excluded from the vegetation profiles (Figure 14).

The relationship between bird species and foliage height diversities can be used predictively. Lines were calculated (Figure 22) to give the 95% confidence limits for the bird species diversity which could be expected in any woodland area where the foliage height diversity is known (and is measured in the same way as in this study). These confidence limits could probably be applied in order to predict the bird species diversity in any woodland in Northern Britain comparable to the census plots studied.

Järvinen & Väisänen (1973) studied the species diversities of bird populations censused throughout Finland by Merikallio (1958) and others. Their extensive data were based on the line transect method, although they pointed out that this method suffered from several weaknesses. They did not have data for the diversities of the vegetation structures of the transect areas. They found that the bird species

diversity decreased from the south to the north, and they used the diversities in the construction of a zoogeographical zonation of Finland. No such geographical differences were found here between the Dumfries-shire and Inverness-shire study areas, but the distance between them (200 km) was much less than those involved in the Finnish study, which encompassed a range of 1200 km.

3.8.10 Discussion: density

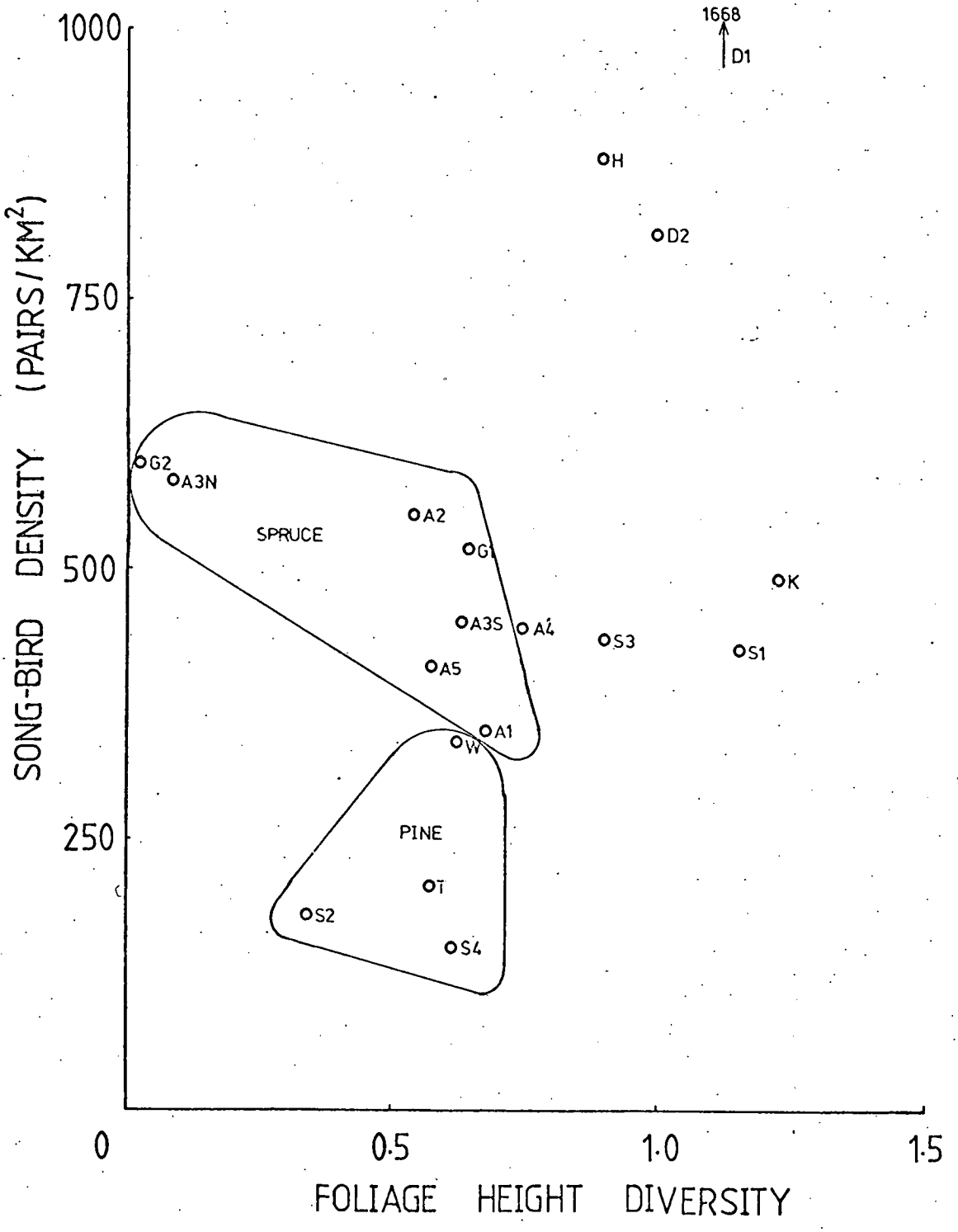
The three most important factors which have been found by others to influence song-bird density in woodlands are vegetation structure, tree species, and soil fertility (von Haartman 1971).

The vegetation structure (measured by the foliage height diversity) did not have a significant effect on the mean total densities on the plots studied ($r = 0.358$, 16 d.f., not significant). When density was plotted against foliage height diversity (Figure 23), the pine and the spruce plantation plots formed two groups, since the density in pine was generally only half that in spruce (the exception, plot W, benefited from an edge effect, as mentioned earlier). The five semi-natural plots could not be grouped, since all had high foliage diversities, while there was a four-fold range in density.

These results indicated that among the plots studied here, vegetation structure was less important as an influence on total density than was the tree species. The exception was the difference between the semi-natural pine wood (S1) and the pine plantations (S2 and S4) in the Spey valley. Several authors have found that in equivalent woodlands, densities are higher in broad-leaved than in coniferous woods, and higher in spruce than in pine (for example: Novikov (1960), USSR; Williamson (1969), Scotland; Eriksson et al (1971), Sweden; and review by von Haartman (1971), Finland). The same gradation was found in the present study between the Annan valley mixed woods, the

FIGURE 23 - THE RELATIONSHIP BETWEEN TOTAL SONG-BIRD DENSITY AND FOLIAGE HEIGHT DIVERSITY.

Each point is marked with the plot identification, and the spruce and pine plantation plots are grouped.



spruce plantations, and the pine plantations. The superiority of densities in birch compared with pine might have explained the difference in density between plots K and H (sub-section 4 above).

Soil fertility was judged by the land class for each plot from the Ordnance Survey Land Classification Map (1945). Most of the plots (Table 19) were on poor quality hill ground (class 8), but those in the Annan valley were on good or medium land (classes 4 & 6). No differences were apparent between bird densities due to the different land classes. Haapanen (1965) worked in forests growing on a wide range of soil types, which he classified according to their underlying vegetation. He found marked differences in total densities in climax forests of different soil fertilities.

To summarise, total bird density on the plots studied depended mainly on the dominant tree species, but little on the vegetation structure except where differences in structure between plots of the same tree species were particularly great.

3.9 The relationships between the commoner species and their habitats on the census plots

All the common species on the census plots were insectivorous (the Chaffinch is granivorous in winter, but insectivorous during the breeding season (Newton 1972b)). Reference should be made to Table 31 throughout.

Goldcrest was entirely dependent on conifers, especially spruce. In the other plots it was restricted to where evergreen conifers grew, while in pole-stage spruce (30-50 years old) its density was proportional to the density of needles. Density was significantly correlated with the percentage of the horizontal area covered by the canopy, which was measured for each plot (Figure 14) ($r = 0.892$, 4 d.f., $P < .02$, Figure 24). Its density was considerably lower in the sparser needled pines. Goldcrests remained in the forests all year round.

Chaffinch is able to nest in many types of tree, and is unspecialised in its feeding habits (Haapanen 1966, Newton 1972b). It was the most widespread species censused, and made up over 10% of the total bird population on every plot, although it was at greatest densities in broad-leaved woods. In winter it moved out of the plantations to feed in flocks in fields.

Wren found most of its requirements close to the ground, and so was dependent on the shrub and ground layer vegetation. In spruce plantations it benefited from brash on the forest floor, and was probably the only species able to exploit this feature of the habitat; thus Wren density on the spruce plots was correlated ($r = 0.705$, 6 d.f., $P = .05$) with the amount of cover measured below the height of 2 m (Figure 25), almost all of which was due to brash. In pine plantations Wren density was also correlated ($r = 0.982$, 2 d.f., $P < .02$) with the amount of vegetation found below 2 m (Figure 25), which was

FIGURE 24 - THE RELATIONSHIP BETWEEN GOLDCREST DENSITY AND THE PERCENTAGE OF CANOPY COVER

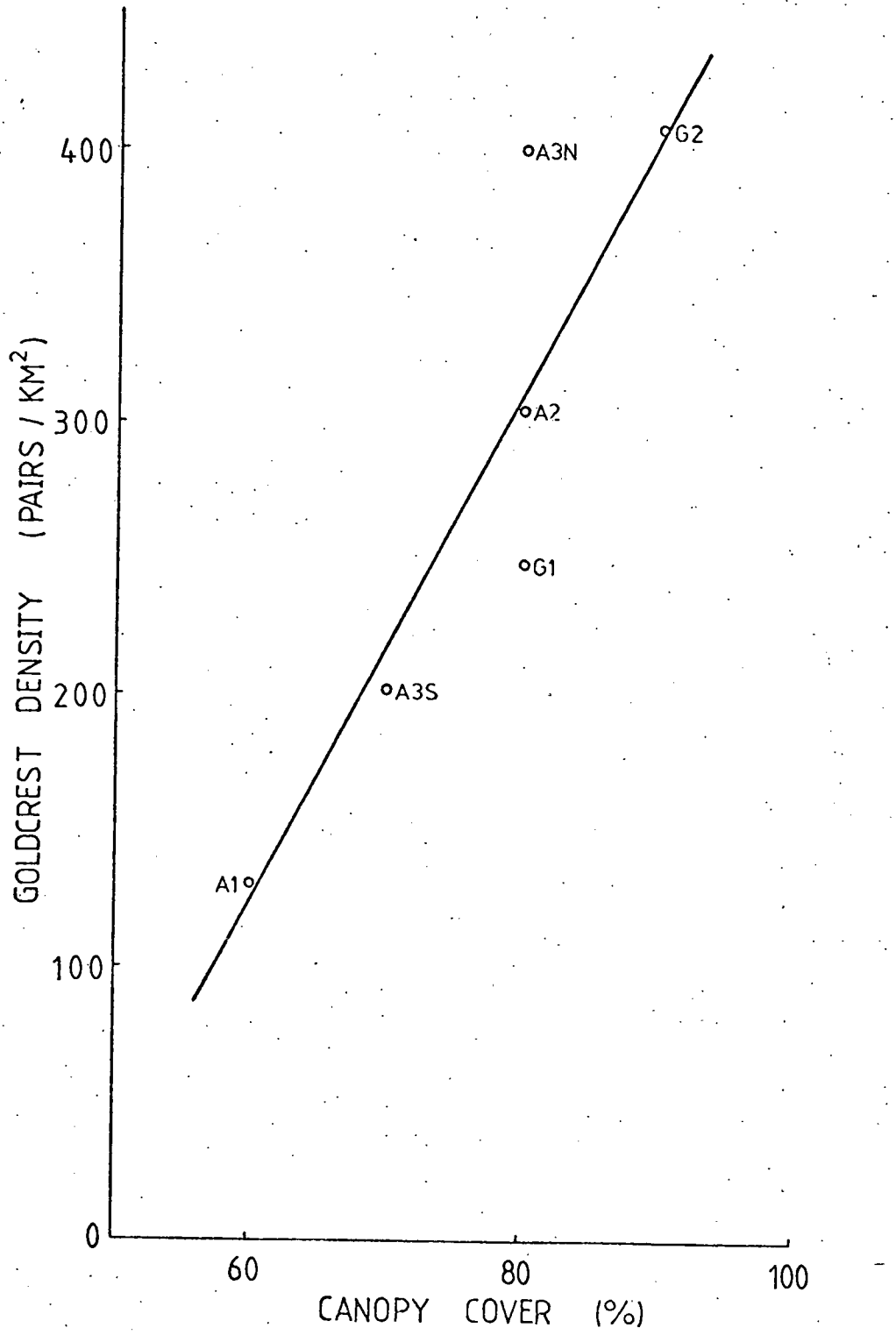
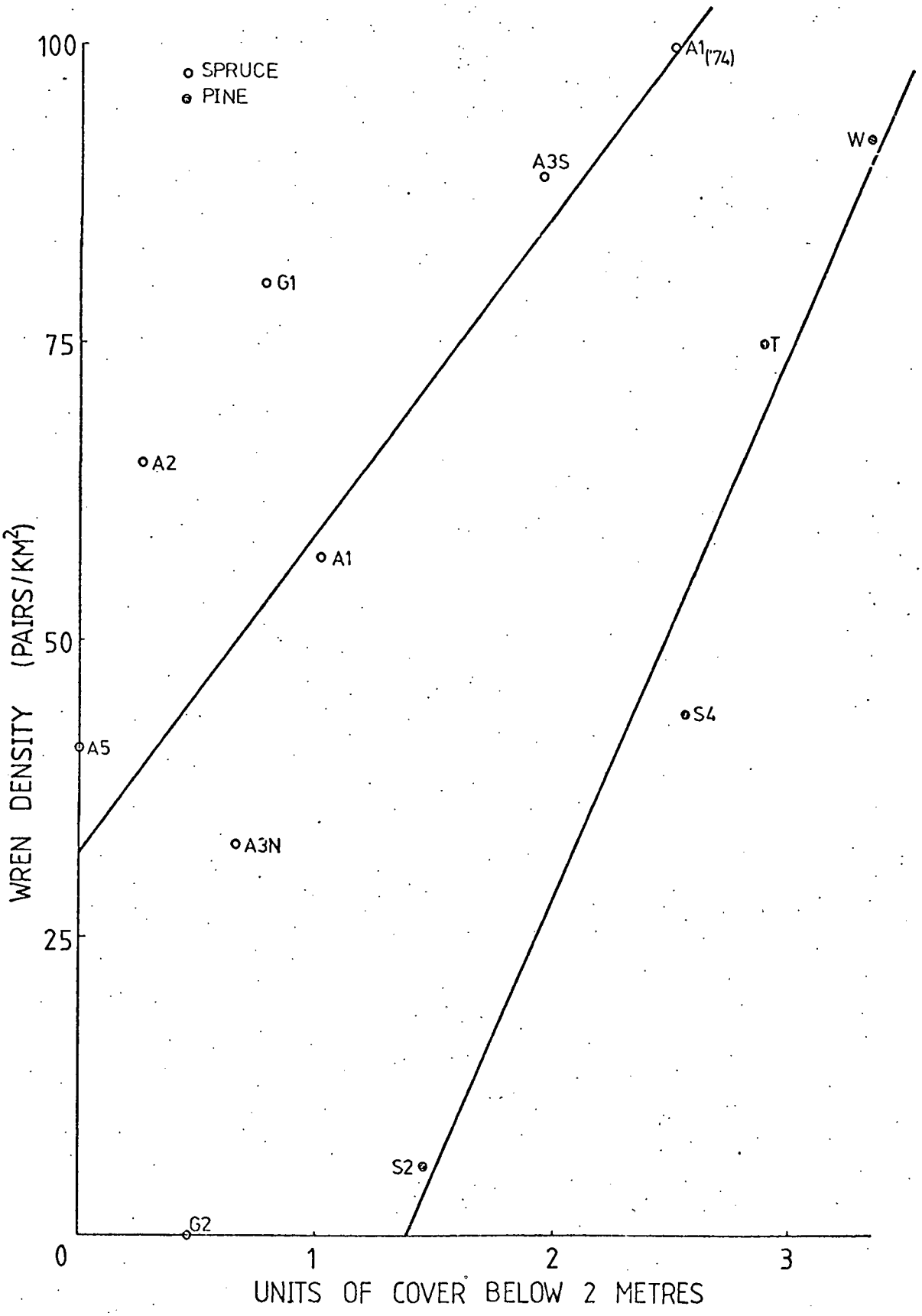


FIGURE 25 - THE RELATIONSHIP BETWEEN WREN DENSITY IN PLANTATIONS AND THE AMOUNT OF LOW-LEVEL COVER, MEASURED FROM THE VEGETATION PROFILES (Figure 14)



mainly Calluna in the Spey valley plots, Bramble and Calluna in the Annan valley.

Coal Tit is found in conifers, although not as exclusively as the Goldcrest. It is a hole-nesting species, but can use a crevice on the ground at the base of a tree and so is probably not limited by shortage of nest sites. In coniferous plantations Coal Tits winter in foraging flocks, often of more than 50 birds (Gibb 1960, pers. obs.). It held much larger territories than Goldcrest, and so occurred at much lower densities.

Robin is particularly a bird of understorey, feeding on the ground or in low shrubs or trees. In winter Robins are partial migrants. The density of Robins reached 45 pairs/km^2 in the older spruce plantations on plot A1 in 1974, although on the same plot in the previous year it was much more scarce. Like Wrens, Robins took advantage of the extensive wind-blown areas there in 1974. Robin density was higher in the regenerating birch/pine scrub with abundant shrub layers, and reached greatest numbers in the mixed wood (D1).

Willow Warbler was the only common summer visitor on the plots. It was absent from the mature spruce plantations, although Village (1974) found a density of 75 pairs/km^2 in a 21 year-old spruce plot in Ae Forest which was bordered by a stream with a fringe of hardwood trees. On the natural pine plot, where the density was about 50 pairs/km^2, it may have been feeding mostly in the scattered birches and rowans. Willow Warbler was the commonest bird of the birch/pine scrub, and was also numerous on the birch plot (S3).

Treecreeper was widely distributed amongst the plots, but occurred in very small numbers. It held at least part of a territory on every plot except the two Greskine Forest plots, the thicket stage spruce, the birch, and one pine plantation (S4). The only plot

with greater numbers of Treecreepers was the mature mixed woodland, where there were four pairs in 1975. This plot provided food and nest sites on the many mature hardwood trees.

Thrushes (Song Thrush, Mistle Thrush and Blackbird) were difficult to census. They were sparsely distributed in conifer plots, and territories there were often larger than the plots. Even on the birch/pine scrub their numbers were low, but they may have been underestimated, since in three places active nests (two Song Thrush and one Mistle Thrush) were found where no bird had been heard singing.

Siskin and Crossbill, unlike all the other species censused, held very small territories within colonial groups, and flocked even in the breeding season. Their species maps could not be interpreted in the same way as those of other species, but estimates were made of the number of pairs which occupied each census plot, by counting the number of individual observations made during census visits. Both species were found throughout the spruce forests, although numbers fluctuated markedly from plot to plot and year to year. This was particularly true in the Spey valley, where Siskins increased from 6 to 46 pairs/ km^2 on plot S1 from 1973 to 1974. These two species are nomadic, and move to areas where their food (conifer seeds) is abundant, so that such fluctuations are known to occur often (Newton 1972b).

3.10 Census results of other workers

Although the B.T.O. Common Birds Census has been in operation for 14 years, most of the work has been near to the most densely populated parts of Britain, and little has been published which is relevant to the present study. The bulk of the census results in the literature derive from Scandinavia, and are of limited relevance here. They were reviewed by von Haartman (1971). Of the census work which has been performed in Scotland, the studies by Yapp (1962, 1974) and Simms (1971) used the line transect method and could only be compared with the transect results given here. The area counts of Watson (1969) could not be compared with results obtained by different methods in the present study. There remain a few mapping censuses which are relevant for discussion in comparison with results obtained in the present study.

Yapp (1962) made transects in semi-natural pine stands in Rothiemurchus and Glenmore Forests, Inverness-shire. The chief differences between his results and those obtained by transects in 1973 on plot S1 were in the relative abundances of Goldcrest (3% of Yapp's total, 13% on plot S1) and Wren (2% and 24% respectively). The two sets of fieldwork were separated by over ten years, and relative numbers of these species may have changed during this time. Increases in numbers of both Goldcrest and Wren up to 1973 were associated with a series of mild winters (e.g. Batten & Marchant 1975). Densities could not be derived from Yapp's transects.

Simms (1971) also gave transect data, derived from a number of pine plantations in Northern Scotland. He found relative abundances of the various species which were similar to those obtained on plot S2, although he too recorded Goldcrests much less often than I did. In spruce plantations Simms (1971) found that Woodpigeons comprised

38-47% of the birds observed. On the transects made in spruce in the present study, Woodpigeons reached only 2-3% of the totals (these data were omitted from Table 24, which only concerned territorial species). This considerable difference is difficult to understand, unless the pigeons on Simms' transects were roosting in large numbers, but were not breeding there. Chaffinch was by far the commonest of the other species on his transects, and Goldcrest and Wren were again under-recorded compared with the transect results obtained in Ae Forest, perhaps for the same reason as given above.

The first plot of Williamson (1969) in Wester Ross (Table 32) was similar to the Spey valley semi-natural plot S1 in structure, but the total bird density was half as great on Williamson's plot. It is difficult to draw any conclusion from this comparison since five years elapsed between the censuses, during which time, as mentioned above, numbers of many species increased generally. Williamson's birch plot, censused at the same time, was considerably richer in birds than the birch plot S3. In this case the Wester Ross wood was presumably much more diversely structured, with a better understorey layer, than the Spey valley plot. Note the high percentage representation of Willow Warbler in Williamson's plot compared with S3, where it was less numerous than the Chaffinch. Williamson's (1974) plots in mixed broad-leaved woodland at Loch Lomond showed high bird densities, of the same order as those in the similarly diverse mixed woodland plot in the Annan valley (D1).

The remaining results quoted in Table 32, all of unpublished work, are particularly relevant to the present study, as they were planned in relation to it. Those of Village (1974) were from Sitka Spruce in the thicket stage (21 years old) in the Ae Forest, similar in structure to plot A5, but at a much lower altitude (180-210 m). It included a

TABLE 32 - RELEVANT CENSUS RESULTS OBTAINED USING THE MAPPING METHOD BY WORKERS OTHER THAN THE AUTHOR. Because of their localities, the last three are especially relevant.

Author	Location of plot	Dominant tree species	Understorey layer	Type	Density prs/km^2	Percentage occurrences of commonest species
Williamson (1969)	Loch Maree, Wester Ross	Scots Pine	Dense Calluna and Vaccinium	Semi-natural	217	Wren 23% Coal Tit 14% Chaffinch 11% Redstart 9% Goldcrest 9% Redpoll 9%
Williamson (1969)	Loch Maree, Wester Ross	Scots Pine	Broad-leaved regeneration (fenced)	Semi-natural	444	Willow Warbler 19% Wren 12% Chaffinch 11% Robin 10% Goldcrest 10% Redpoll 10%
Williamson (1969)	Loch Maree, Wester Ross	Birch	Calluna and Vaccinium	Semi-natural	1100	Willow Warbler 39% Chaffinch 15% Wren 14%
Williamson (1974)	Loch Lomond	Mixed broad-leaved	Bramble, Bracken, grasses, Vaccinium	Semi-natural	1480	Chaffinch 18% Wren 15% Willow Warbler 10% Robin 8% Blackbird 8% Blue Tit 5%
Village (1974)	Ae Forest 180-210 m a.s.l.	Sitka Spruce Land class 6/8	None	Planted 1953	486	Goldcrest 40% Willow Warbler 15% Chaffinch 15% Robin 10% Coal Tit 9% Wren 7%
Smith, R.E.N. (pers. comm. 1974)	Irvineburn, Esk valley, Dumfries-shire 75-90 m a.s.l.	Norway Spruce Land class 6	Brashings	Planted c.1935	1219	Goldcrest 38% Wren 20% Chaffinch 18% Robin 7% Coal Tit 5%
Malster (1975)	Rothiemurchus Forest, Spey valley 360-500 m a.s.l.	Scots Pine Land class 8	Scattered Juniper; Calluna and Vaccinium	Semi-natural	395	Chaffinch 28% Goldcrest 22% Wren 20% Coal Tit 10% Tree Pipit 5%

narrow valley with a few old broad-leaved trees on its banks. The densities of the five major species on plot A5 (Goldcrest, Chaffinch, Robin, Coal Tit and Wren) were similar on Village's plot, but he also found Willow Warbler at a density of 75 pairs/km^2, which was absent from A5. This could be due to a lack of nest sites or to insufficient food on the higher plot.

The plot censused in 1974 by Smith (pers. comm.) in the Esk valley, Dumfries-shire, was of Norway Spruce similar in structure to plots A2 and A3, with ground cover only of brashings. The plot was 75-90 m above sea level. The total bird density was more than twice that on the comparable Ae Forest plots. While Goldcrest was still the commonest species, it was less dominant than in Ae Forest, since densities of Wren, Chaffinch, and Robin were around three times as great in Eskdale as in Ae. Some caution must be exercised in comparing results from different observers, but there can be no doubt that the Eskdale plantation held a considerably greater density of birds than Ae Forest. This can be explained in part by the position of the Eskdale plot - which formed one half of a narrow planting in a tributary valley of the Esk, the plot being bounded on one side by pasture fields - and also by its lower altitude and richer soil than that of the Ae plots. The small size of the Eskdale plantation would have led to higher densities due to increased edge effect (Odum 1971).

Malster (1975) censused two plots of semi-natural pine wood in Rothiemurchus Forest, Inverness-shire. Both were similar to the Abernethy Forest plot S1, but were at higher altitudes. They had similar bird communities and densities to that plot, the only difference being the absence of Willow Warblers from Malster's plots.

CHAPTER 4

THE RELATION OF THE SPARROWHAWK TO ITS PREY

4.1 Prey samples at the nests studied

Prey remains found on nests in the form of carcasses, feathers, or legs were identified whenever possible, and feathers and legs were also found and identified at plucking posts near nests. The prey data collected on nest visits were considerably supplemented with data collected at the same sites by I. Newton and M. Marquiss. The numbers of items from different nests varied greatly, because at some nests there were frequently used plucking posts or numerous prey remains on the nest, while at others no plucking post could be found, and the nest was kept clear of prey remains.

The prey samples collected in this manner did not necessarily give an accurate estimate of the composition of the prey, especially during the later part of the nestling period, because the smaller species, such as Goldcrest and Wren, were often consumed completely, so that no trace was left, while this was not the case with larger species, such as thrushes. The legs of thrushes and larger birds were often found on the nests. These biases, which applied to all nests, must be borne in mind for the remainder of this section.

The Sparrowhawks' prey encompassed a wide range of bird species. The total of 1358 bird items included 49 different species (Table 33), but many were represented by few individuals. Mammals, of which the majority were Bank Voles, accounted for 3% by numbers of the total sample.

There were several interesting contrasts between Ae Forest and Annan valley areas (Table 33): Robin, Wren, and Goldcrest were all taken much more frequently in the forest than in the valley (28% and

TABLE 33 - THE COMPOSITION OF PREY SAMPLES FROM SPARROWHAWK SITES IN EACH AREA, DETERMINED FROM PREY REMAINS AT PLUCKING POSTS AND ON NESTS

	Area:								
	Remote	Central	Edge	St Ann's	Templand	Moffat	Ae Forest	Annan Valley	Total
Number of items	268	302	321	261	223	26	891	484	1401
Number of bird species	23	27	31	28	34	10	40	37	49
Mean bird weight (grams)	45	48	63	80	58		52	70	59
Mean bird weight, excluding pigeons	31	39	40	50	51		37	51	42
% forest species[1]	59	56	51	31	32	(36)	55	32	47
Chaffinch (% of total)	17	27	23	20	17		22	19	21
Robin	14	16	12	7	9		14	8	12
Song Thrush	5	9	8	11	12		8	11	9
Blackbird	2	6	5	16	14		5	15	8
Wren	12	7	6	2	4		8	3	6
Woodpigeon	4	2	6	8	2		4	5	4
Goldcrest	9	3	6	0	0		6	0	4
Meadow Pipit	9	4	2	1	0		5	1	3
Willow Warbler	5	3	4	1	2		5	1	3
Starling	2	2	3	3	5		2	4	3
Mistle Thrush	2	2	1	2	6		2	4	2
Blue Tit	-	1	2	6	3		1	4	2
Coal Tit	4	2	2	1	-		3	1	2
Waders	2	2	3	2	5		2	4	3
Other birds	7	11	12	16	19		10	17	13
Bank Vole	3	2	2	2	1		3	1	2
Other mammals	1	1	1	1	-		1	0	1

[1] Percentage of bird prey made up by the five commonest forest species: Goldcrest, Chaffinch, Wren, Coal Tit and Robin.

11% of the totals respectively), while the reverse held for the three larger thrushes (15% and 30% respectively). These results showed that the prey was to some extent related to availability in the nest area, since the first three species were most numerous in the forest, while the thrushes were scarce there but common in hedgerows and scrubby deciduous woods in the valley. The Chaffinch, abundant in both major areas, was the most numerous species in the prey samples in every area studied.

The species found in the prey samples reflected the species available in each area, so that a larger number of species (34) was found in the Templand area, where the habitats were more diverse, than in the remote Ae Forest (23 species). The wide range of species found showed that Sparrowhawks were opportunist hunters with specialised methods. The same conclusion was drawn on the basis of prey samples by Uttendörfer (1939), Tinbergen (1946), and van Beusekom (1971).

The species which were more commonly taken in the valley area were on the whole larger birds than those in the forest, so that the mean biomass of bird prey items was 70 grams in the valley, and 52 grams in the forest (Table 33). There was also a difference between the edge of the forest and the other two forest areas. However the biomass calculations were affected by the differing numbers of a few large species such as Woodpigeon, since one pigeon was equivalent in weight to about 80 Goldcrests. This explained the difference between the St Ann's area, where there were 22 pigeons in the sample, and Templand, with only 4 Woodpigeons. However when pigeons were excluded from the calculations, the mean weight of bird prey was still higher in the valley than in the forest (51 g and 37 g respectively, Table 33).

The prey samples were thought not to be representative of the absolute numbers of prey taken by the Sparrowhawks, and prey was also

captured in a wider range of habitats than those censused. Therefore it was only possible to compare the species composition of the prey samples with the census results in general, so as to examine whether prey was captured at random, or whether certain species were more vulnerable than others. For example, the three thrush species formed under 2% of the populations of the forest plots, yet 15% of the prey there. This would suggest that forest dwelling thrushes were highly vulnerable to predation, or that forest Sparrowhawks caught thrushes outside the forest. Similarly the Willow Warbler, which in the forest area was restricted to young plantings, was predated much more heavily there than in the valley area, where it was the most numerous species on most of the plots censused.

4.2 Growth rates in relation to local prey densities

It was suggested earlier (p.179) that in remote areas poor growth rates and high mortality of the nestlings, as well as poor parental care, were linked with a poor local food supply and remoteness of the nests from habitats which provided rich sources of prey.

Densities of song-birds were available in one or more years from six plots in Ae Forest (including that of Village (1974)), of which two were in each of the sub-areas first described in section 2.7, and from three woods containing nest sites and three other woods in the Templand area of the Annan valley (Figure 26). Typical weights of the various song-bird species were applied to the census data, and the biomass/km^2 of breeding adult song-birds was estimated for each census plot (Figure 26). There were no great differences in density or biomass between the Ae Forest areas, and both densities and the biomasses in the Templand area nesting (pine) woods were slightly lower than those in Ae Forest.

A direct approach was made to attempt to relate growth rates to prey densities by means of the fixed-time counts, which were made at eight of the Sparrowhawk nest sites in the Ae Forest for which there were also growth data. The correlation between the number of birds recorded on fixed-time counts and the mean rate of weight gain at the eight sites was not significant ($r = 0.260$, 6 d.f.). This result was unreliable, however, because of the bias towards uniformity between sites in the fixed-time method (section 3.6).

Mapping census results suggested that the poor performance of Sparrowhawks in remote and central forest areas was not due to low prey densities there. Nevertheless, prey might have been less easily caught in the dense thicket-stage trees of much of the remote area than in the more mature pine plantations of the Templand area.

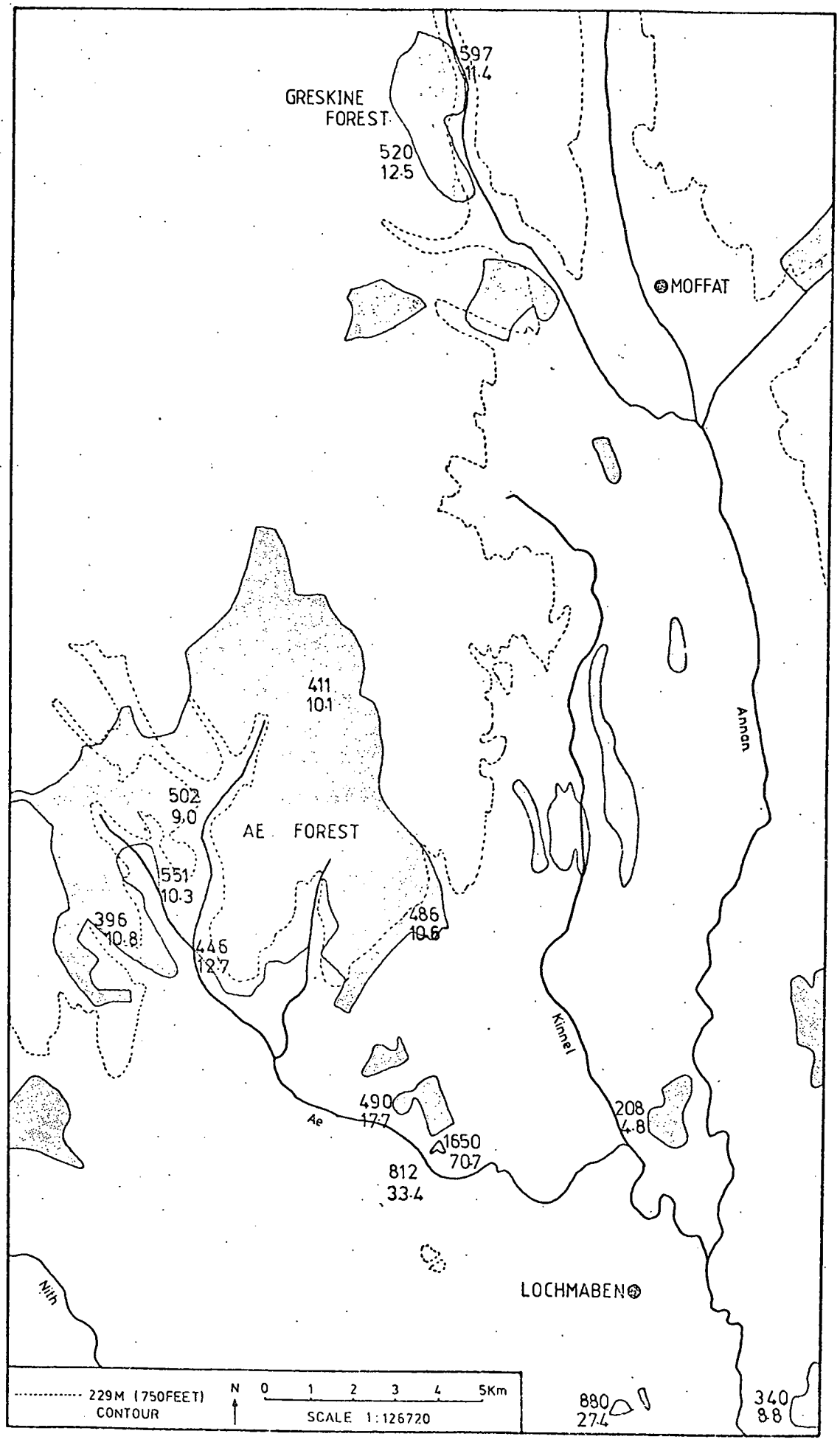


FIGURE 26 - MAP TO SHOW THE DENSITIES (pairs/km^2) AND BIOMASSES (kg/km^2) OF SONG-BIRDS ON CENSUS PLOTS IN DIFFERENT AREAS.

Here, and also in the St Ann's area, which contained a similar mixture of woods and farmland, the Sparrowhawks were breeding close to a number of woods and areas of scrub containing high prey densities. Because these woods held relatively more of the larger song-birds such as thrushes, the biomasses/km^2 in these valley woods were even higher relative to the forest than were the densities. Ae Forest edge birds were only a short flight from several areas of valley woodland and riverside scrub, and so benefited in the same way as the birds nesting in the valley. By contrast in the remote Ae Forest sites, there were no areas nearby which held prey densities higher than the forest around the nest. The unplanted areas to the north-west and north-east of the forest were upland hill ground, which held relatively few birds (such as Meadow Pipits and Skylarks). The Sparrowhawks breeding at remote sites had either to fly long distances to find areas dense in prey, or to concentrate on the sparser prey available in the forest. The birds in the central forest area were in an intermediate position, and could either use the forest or the more limited areas of valley woodland and scrub near the nests, or fly less far than the remote area birds to woods with abundant prey.

A study in 1975 (Newton & Marquiss, in progress), in which six breeding adults were fitted with radio transmitters during the period when they were raising young, showed that two hens nesting in the remote area regularly over-flew other birds' nest-territories to hunt; one of them was frequently found on the edge of the Nith valley, 9 km from her nest. Two hens nesting in the central area and the edge area both travelled much less widely to hunt, although they also frequently left the vicinities of their nests.

The telemetry study, although it was based on a small number of birds and did not include any in valley woods, completed the link between the performance of the forest birds in raising their young and the distance from the nest to rich sources of prey. The prey densities obtained for the nesting areas had little relevance to the mortality and growth rates of nestlings because of the large sizes of the females' hunting ranges. However the census data showed that there were woodlands with high prey densities available in areas where nestling growth rates were high and mortality was low, whereas areas with low growth rates and high mortality were distant from such woods. The differences could be partly explained by the cost of commuting to distant sources of abundant prey, which increased with remoteness, and was manifested by reduced prey capture and poorer parental care. When they did not commute, birds had to rely on low density forest prey, which generally consisted of smaller species which may have been less easily captured.

4.3 Sparrowhawk densities in relation to prey densities

Sparrowhawk nest-territories in Dumfries-shire were on average 0.6 km apart, while in the Inverness-shire study area the spacing averaged 2.2 km (Newton 1972a). The corresponding densities were 2.5 and 0.2 nest-territories per square kilometre respectively.

In the Dumfries-shire area, the remote Ae Forest nest-territories were further apart than those in the central and edge areas of the forest, but the limitation may have been in a lack of suitable nest sites, since the trees in the area were younger and denser growing than those in the other parts of the forest. However the nesting density in the remote area may still have been increased relative to that expected under the poor local conditions, due to the availability of abundant prey in valley woods within range of the nests.

When the Annan valley and Spey valley areas, and their predominant woodland types, were each considered as a whole, the overall bird densities in Annan valley woods were found to be at least twice as great as in the Spey valley woods (p.150). Furthermore, when the best woods in each area were taken, the factor increased to about four times. The importance of remoteness from rich prey sources in limiting the success of Sparrowhawks when raising young in Dumfries-shire suggested that in the Spey valley, Sparrowhawk nesting density was adjusted to the prey availability in the best woods there.

There was thus a positive relationship between the predator density and maximum prey density, but it was not a linear one, since the predator density differed between the two areas by a factor of twelve, whereas the maximum prey density differed only by a factor of four. It appeared that prey density and availability as prey did not correspond closely.

ACKNOWLEDGEMENTS

I am indebted to Dr Ian Newton, one of my supervisors, for giving me the opportunity to undertake this project, and for his constant advice and encouragement which were freely given throughout its course. Not only did he offer support during the field seasons, and in particular find the locations of most of the Sparrowhawk nests which I studied, but he has also given constructive criticism of the entire manuscript of this thesis.

I am grateful to the successive professors of Forestry and Natural Resources, Prof. F.T. Last and Prof. P.G. Jarvis, for the facilities of the department, from which I have benefited greatly, and to many members of the department with whom I have had useful discussions. In particular, my thanks are extended to Dr J.D. Lockie, my supervisor within the department, for his help at many stages during the study, and for reading the manuscript of the thesis. I also wish to thank my father for considerable assistance with the editing of the manuscript.

The fieldwork could not have been achieved without the co-operation of the many landowners and their agents on whose land I have worked, and in particular that of the Forestry Commission, who also allowed me to live on their land. I wish to express my gratitude for their support to Mr Alan Young and his staff at Ae Forest Office. I also appreciated the help in Dumfries-shire of Mr Mick Marquiss.

I am pleased to acknowledge the advice and hospitality of Hon. D.N. Weir during my visits to work in the Spey valley, and to thank the successive wardens of the R.S.P.B. reserve at Loch Garten who extended to me the facilities of the wardens' camp there.

Mr L.A. Batten kindly interpreted some of my census maps as a test of consistency, and Mr D. Brown gave statistical advice.

I wish to thank the following who made their unpublished work available: John Malster, Angela Mulliner, Virginia Reeves, Roger Smith, Andrew Village, and my brother, Martin Moss, with whom I also had many helpful discussions.

This study was made possible by two years financial support in the form of a Biological Scholarship from the Nuffield Foundation, and I am grateful to the Trustees and to the Fellowships Adviser, Mr D.D. Yonge. For the third year's funding I acknowledge the N.E.R.C., who awarded a research grant to Dr Lockie.

BIBLIOGRAPHY

ALEXANDER, C.J. & ALEXANDER, H.G. (1909). On a plan of mapping migratory birds in their nesting areas. British Birds 2: 322-326.

ANDERSON, D.R. & POSPAHALA, R.S. (1970). Correction of bias in belt transect studies of immotile objects. Journal of Wildlife Management 34: 141-146

BATTEN, L.A. & MARCHANT, J.H. (1975). Bird population changes for the years 1972-3. Bird Study 22: 99-104

BELL, B.D., CATCHPOLE, C.K. & CORBETT, K.J. (1968). Problems of censusing Reed Buntings, Sedge Warblers and Reed Warblers. Bird Study 15: 16-21

BEST, L.B. (1975). Interpretational errors in the "mapping method" as a census technique. Auk 92: 452-460

van BEUSEKOM, C.F. (1971). Sperwervoedsel: een steekproef uit de zangvogelwereld. De Levende Natur 74: 13-22

BLONDEL, J., FERRY, C. & FROCHOT, B. (1970). La méthode des indices d'abondance (I.P.A.) ou des relevés d'avifaune par "stations d'écoute". Alauda 38: 55-71

BRECKENRIDGE, W.J. (1935a). A bird census method. Wilson Bulletin 47: 195-197

BRECKENRIDGE, W.J. (1935b). An ecological study of some Minnesota Marsh Hawks. Condor 37: 268-276

BROSSET, A. (1973). Évolution des Accipiter forestiers de l'est du Gabon. Alauda 41: 185-201

BROWN, L.H. & AMADON, D. (1968). Eagles, Hawks and Falcons of the World. Country Life Books, Feltham, Middlesex

BRYANT, D.M. (1972). The breeding biology of the House Martin (Delichon urbica L.) in relation to aerial insect abundance. Ph.D. thesis, University of London

BULMER, M.G. & PERRINS, C.M. (1973). Mortality in the Great Tit. Ibis 115: 277-281

CAVÉ, A.J. (1968). The breeding of the Kestrel Falco tinnunculus L. in the reclaimed area Oostelijk Flevoland. Netherlands Journal of Zoology 18: 313-407

CLAPHAM, A.R., TUTIN, T.G. & WARBURG, E.F. (1968). Excursion Flora of the British Isles. 2nd edition. Cambridge University Press, Cambridge

COLQUHOUN, M.K. (1940a). The density of woodland birds determined by the sample count method. Journal of Animal Ecology 9: 53-67

COLQUHOUN, M.K. (1940b). Visual and auditory conspicuousness in a woodland bird community: a quantitative analysis. Proceedings of the Zoological Society of London A 110: 129-148

DAWSON, W.R. & EVANS, F.C. (1957). Relation of growth and development to temperature regulation in nestling Field and Chipping Sparrows. Physiological Zoology 30: 315-327

DAWSON, W.R. & EVANS, F.C. (1960). Relation of growth and development to temperature regulation in nestling Vesper Sparrows. Condor 62: 329-340

EBERHARDT, L.L. (1968). A preliminary appraisal of line transects. Journal of Wildlife Management 32: 82-88

EMLEN, J.T. (1971). Population densities of birds derived from transect counts. Auk 88: 323-342

ENEMAR, A. (1959). On the determination of the size and composition of a passerine bird population during the breeding season. Vår Fågelvärld suppl. 2: 1-114

ENEMAR, A. (1962). A comparison between the bird census results of different ornithologists. Vår Fågelvärld 21: 109-118

ENEMAR, A. & SJÖSTRAND, B. (1967). The strip survey as a complement to study area investigations in bird census work. Vår Fågelvärld 26: 111-126

ERIKSSON, C-G., NILSSON, L. & SVENSSON, B. (1971). The passerine bird fauna of some forest habitats in Stora Sjöfallet National Park, Swedish Lapland. Bird Study 18: 21-26

GIBB, J.A. (1960). Populations of tits and Goldcrests and their food supply in pine plantations. Ibis 102: 163-208

HAAPANEN, A. (1965-6). Bird fauna of the Finnish forests in relation to forest succession. Annales Zoologici Fennici 2: 153-196, 3: 176-200

von HAARTMAN, L. (1971). Population dynamics. In Farner, D.S. & King, J.R. (eds.), Avian Biology 1: 392-459. Academic Press, London

HALD-MORTENSEN, P. (1974). (Nest and nest site of the Sparrowhawk Accipiter nisus - and some comparisons with the Goshawk A. gentilis) Dansk Ornithologisk Forenings Tidsskrift 68: 91-115

HARRIS, M.P. (1966). The breeding biology of the Manx Shearwater Puffinus puffinus. Ibis 108: 17-33

HAUKIOJA, E. (1968). Reliability of the line survey method in bird census with reference to Reed Bunting and Sedge Warbler. Ornis Fennica 45: 105-113

HOGSTAD, O. (1967). Factors influencing the efficiency of the mapping method in determining breeding bird populations in conifer forests. Nytt Magasin for Zoologi 14: 125-141

HOWELL, J.C. (1951). The roadside census as a method of measuring bird populations. Auk 68: 334-357

INTERNATIONAL BIRD CENSUS COMMITTEE (1969). Recommendations for an international standard for a mapping method in bird census work. Bird Study 16: 248-255

JÄRVINEN, O. & VÄISÄNEN, R.A. (1973). Species diversity of Finnish birds, I. Zoogeographical zonation based on land birds. Ornis Fennica 50: 93-125

JÄRVINEN, O. & VÄISÄNEN, R.A. (1975). Estimating relative densities of birds by the line transect method. Oikos 26: 316-322

KRAMER, V. (1955). Habicht und Sperber. Neue Brehm Bücherei, Ziemsen Verlag

KRZANOWSKI, A. (1964). (The aural stationary record - a quick method of quantitative studies of forest avifauna). Ekologia Polska Series B 10: 221-233

LACK, D. (1937). A review of bird census work and bird population problems. Ibis 79: 369-395

LACK, D. (1954). The natural regulation of animal numbers. Clarendon Press, Oxford

LACK, D. (1966). Population studies of birds. Clarendon Press, Oxford

LACK, D. (1968). Ecological adaptations for breeding in birds. Methuen, London

LACK, D. & LACK, E. (1951). The breeding biology of the Swift Apus apus. Ibis 93: 501-546

LACK, D. & SILVA, E.T. (1949). The weight of nestling Robins. Ibis 91: 64-78

LACK, D. & VENABLES, L.S.V. (1939). The habitat distribution of British woodland birds. Journal of Animal Ecology 8: 39-71

LEES, J. (1949). Weights of Robins. Ibis 91: 79-88, 287-299

LIVERSIDGE, R. (1962). The breeding biology of the Little Sparrowhawk Accipiter minullus. Ibis 104: 399-406

MACARTHUR, R.H. & MACARTHUR, J.W. (1961). On bird species diversity. Ecology 42: 594-598

MACARTHUR, R.H., RECHER, H.F. & CODY, M.L. (1966). On the relation between habitat selection and species diversity. American Naturalist 100: 319-327

MAHER, W.J. (1964). Growth rate and development of endothermy in the Snow Bunting (Plectrophenax nivalis) and Lapland Longspur (Calcarius lapponicus) at Barrow, Alaska. Ecology 45: 520-528

MALSTER, J. (1975). Breeding birds of pinewoods in Rothiemurchus Forest. Unpublished report, Nature Conservancy Council, Aviemore

MERIKALLIO, E. (1958). Finnish birds: their distribution and numbers. Fauna Fennica 5: 1-181

MOSS, M. (1975). Feeding behaviour and development of young at a Sparrowhawk nest, 1975. Unpublished report, Institute of Terrestrial Ecology, Edinburgh

MULLINER, A.M. & REEVES, V. (1974). Feeding behaviour and development of young at two Sparrowhawk nests, 1974. Unpublished report, Durham University

NEWTON, I. (1972a). Birds of prey in Scotland: some conservation problems. Scottish Birds 7: 5-23

NEWTON, I. (1972b). Finches. Collins, London

NEWTON, I. (1973a). Success of Sparrowhawks in an area of pesticide usage. Bird Study 20: 1-8

NEWTON, I. (1973b). Studies of Sparrowhawks. British Birds 66: 271-278

NEWTON, I. (1974). Changes attributed to pesticides in the nesting success of the Sparrowhawk in Britain. Journal of Applied Ecology 11: 95-102

NEWTON, I. (1976). Breeding of Sparrowhawks (Accipiter nisus) in different environments. Journal of Animal Ecology 45:

NEWTON, I. & BOGAN, J.A. (1974). Organochlorine residues, eggshell thinning and hatching success in British sparrowhawks. Nature 249: 582-583

NEWTON, I. & MOSS, D. (in press). Breeding birds of Scottish pinewoods. Symposium on the Pinewoods of Scotland

NOVIKOV, G.A. (1960). (The geographical variability of the population density of forest birds in the European part of the U.S.S.R. and adjacent countries.) Zoologicheskii zhurnal 39: 433-447

O'CONNOR, R.J. (1973). Growth and metabolism in some insectivorous birds compared with a granivorous species. D.Phil. thesis, University of Oxford

O'CONNOR, R.J. (1975). Growth and metabolism in nestling passerines. In Peaker, M., (ed). Advances in avian physiology. Symposia of the Zoological Society of London 35: 277-306

ODUM, E.P. (1971). Fundamentals of Ecology. 3rd edition. Saunders, Philadelphia

OWEN, J.H. (1915-1936). Some breeding habits of the Sparrowhawk (and other similar titles). British Birds 8: 193-195; 10: 2-10; 10: 26-37; 10: 50-59; 10: 74-86; 10: 106-115; 12: 61-66; 12: 74-82; 13: 114-124; 15: 74-77; 20: 114-120; 25: 151-155; 25: 238-243; 26: 34-40; 30: 22-26

PALMGREN, P. (1930). Quantitative Untersuchungen über die Vogelfauna in den Waldern Südfinnlands mit besonderer Berücksichtigung Ålands. Acta Zoologici Fennici 7: 1-218

PETERSON, R., MOUNTFORT, G. & HOLLOM, P.A.D. (1966). A field guide to the birds of Britain and Europe. 2nd edition. Collins, London

PIELOU, E. (1969). An Introduction to Mathematical Ecology. Wiley, New York

PIELOWSKI, Z. & WASILEWSKI, A. (1972). The regulation of numbers and certain aspects of the population structure in communities of forest birds. Ekologia Polska 20: 219-252

PRESTT, I. (1965). An enquiry into the recent breeding status of some of the smaller birds of prey and crows in Britain. Bird Study 12: 196-221

RATCLIFFE, D.A. (1970). Changes attributable to pesticides in egg breakage frequency and eggshell thickness in some British birds. Journal of Applied Ecology 7: 67-115

RECHER, H.F. (1969). Bird species diversity and habitat diversity in Australia and North America. American Naturalist 103: 75-80

REYNOLDS, R.T. (1972). Sexual dimorphism in Accipiter hawks: a new hypothesis. Condor 74: 191-197

RICKLEFS, R.E. (1967). A graphical method of fitting equations to growth curves. Ecology 48: 978-983

RICKLEFS, R.E. (1968). Patterns of growth in birds. Ibis 110: 419-451

RICKLEFS, R.E. (1973). Patterns of growth in birds. II. Growth rate and mode of development. Ibis 115: 177-201

SCHARF, W.C. & BALFOUR, E. (1971). Growth and development of nestling Hen Harriers. Ibis 113: 323-329

SCHNELL, J.H. (1958). Nesting behaviour and food habits of Goshawks in the Sierra Nevada of California. Condor 60: 377-403

SEIERSTAD, S., SEIERSTAD, A. & MYSTERUD, I. (1965). Statistical treatment of the 'inconspicuousness problem' in animal population surveys. Nature 206: 22-23

SHANNON, C.E. & WEAVER, W. (1949). The Mathematical Theory of Communication. University of Illinois Press, Urbana

SIMMS, E. (1971). Woodland Birds. Collins, London

SKELLAM, J.G. (1958). The mathematical foundations underlying the use of line transects in animal ecology. Biometrics 14: 385-400

SLAGSVOLD, T. (1973a). Variation in the song activity of passerine forest bird communities throughout the breeding season. Special regard to the Song Thrush Turdus philomelos Brehm. Norwegian Journal of Zoology 21: 139-158

SLAGSVOLD, T. (1973b). Estimation of density of the Song Thrush Turdus philomelos Brehm by different methods based upon singing males. Norwegian Journal of Zoology 21: 159-172

SNOW, D.W. (1965). The relationship between census results and the breeding population of birds on farmland. Bird Study 12: 287-304

SNYDER, N.F.R. & SNYDER, H.A. (1973). Experimental study of feeding rates of nesting Cooper's Hawks. Condor 75: 461-463

STEWART, R.E. & ALDRICH, J.W. (1951). Removal and repopulation of breeding birds in a spruce fir forest community. Auk 68: 471-482

STORER, R.W. (1966). Sexual dimorphism and food habits in three North American Accipiters. Auk 83: 423-436

SUMNER, E.L. (1929). Comparative studies in the growth of young raptores. Condor 31: 85-111

SUMNER, E.L. (1933). The growth of some young raptorial birds. University of California Publications in Zoology 40: 277-308

TAYLOR, S.M. (1965). The common birds census - some statistical aspects. Bird Study 12: 268-286

TINBERGEN, L. (1946). De Sperwer als roofvijand van Zangvogels. Ardea 34: 1-213

UTTENDÖRFER, O. (1939). Die Ernährung der deutschen Raubvögel und Eulen und ihre Bedeutung in der heimischen Natur. Neumann, Neudamm.

VILLAGE, A. (1974). Density changes in small bird populations in maturing woodland. Unpublished report, Durham University

WATSON, A. (1957). The behaviour, breeding, and food-ecology of the Snowy Owl Nyctea scandiaca. Ibis 99: 419-462

WATSON, A. (1969). Preliminary counts of birds in central Highland pine woods. Bird Study 16: 158-163

WILLIAMSON, K. (1964). Bird census work in woodland. Bird Study 11: 1-22

WILLIAMSON, K. (1969). Bird communities in woodland habitats in Wester Ross, Scotland. Quarterly Journal of Forestry 63: 305-328

WILLIAMSON, K. (1974). Oak wood breeding bird communities in the Loch Lomond National Nature Reserve. Quarterly Journal of Forestry 68: 9-28

WILLIAMSON, K. & HOMES, R.C. (1964). Methods and preliminary results of the common birds census, 1962-63. Bird Study 11: 240-256

YAPP, W.B. (1956a). The theory of line transects. Bird Study 3: 93-104

YAPP, W.B. (1956b). The birds of high level woodlands. The Breeding Community. Bird Study 3: 191-204

YAPP, W.B. (1959). The birds of high level woodlands. The winter population. Bird Study 6: 136-140

YAPP, W.B. (1962). Birds and Woods. Oxford University Press, London

YAPP, W.B. (1974). Birds of the northwest Highland birchwoods. Scottish Birds 8: 16-31

APPENDIX 1

SCIENTIFIC NAMES[1] OF BIRD SPECIES MENTIONED

Blackbird	*Turdus merula*
Blackcap	*Sylvia atricapilla*
Bullfinch	*Pyrrhula pyrrhula*
Bunting, Lapland	*Calcarius lapponicus*
Bunting, Reed	*Emberiza schoeniclus*
Bunting, Snow	*Plectrophenax nivalis*
Capercaillie	*Tetrao urogallus*
Chaffinch	*Fringilla coelebs*
Chiffchaff	*Phylloscopus collybita*
Crossbill	*Loxia curvirostra*
Cuckoo	*Cuculus canorus*
Dunnock	*Prunella modularis*
Flycatcher, Spotted	*Muscicapa striata*
Goldcrest	*Regulus regulus*
Goshawk	*Accipiter gentilis*
Greenfinch	*Carduelis chloris*
Harrier, Hen	*Circus cyaneus*
Hawk, Cooper's	*Accipiter cooperii*
Jay	*Garrulus glandarius*
Kestrel	*Falco tinnunculus*
Martin, House	*Delichon urbica*
Owl, Snowy	*Nyctea scandiaca*
Owl, Tawny	*Strix aluco*
Pipit, Meadow	*Anthus pratensis*
Pipit, Tree	*Anthus trivialis*
Redpoll	*Acanthis flammea*
Redstart	*Phoenicurus phoenicurus*
Robin	*Erithacus rubecula*
Shearwater, Manx	*Puffinus puffinus*
Siskin	*Carduelis spinus*
Skylark	*Alauda arvensis*
Sparrow, Field	*Spizella pusilla*
Sparrow, House	*Passer domesticus*
Sparrowhawk	*Accipiter nisus*
Sparrowhawk, Little	*Accipiter minullus*
Starling	*Sturnus vulgaris*
Swift	*Apus apus*

[1] As in Peterson *et al* (1966)

APPENDIX 1 (continued)

Thrush, Mistle	*Turdus viscivorus*
Thrush, Song	*Turdus philomelos*
Tit, Blue	*Parus caeruleus*
Tit, Coal	*Parus ater*
Tit, Crested	*Parus cristatus*
Tit, Great	*Parus major*
Tit, Long-tailed	*Aegithalos caudatus*
Tit, Willow	*Parus montanus*
Treecreeper	*Certhia familiaris*
Wagtail, Grey	*Motacilla cinerea*
Warbler, Garden	*Sylvia borin*
Warbler, Reed	*Acrocephalus scirpaceus*
Warbler, Sedge	*Acrocephalus schoenobaenus*
Warbler, Willow	*Phylloscopus trochilus*
Whitethroat	*Sylvia communis*
Woodpecker, Great Spotted	*Dendrocopos major*
Woodpigeon	*Columba palumbus*
Wren	*Troglodytes troglodytes*
Yellowhammer	*Emberiza citrinella*

MAMMAL:

Bank Vole	*Clethrionomys glareolus*

APPENDIX 2

SCIENTIFIC NAMES[1] OF PLANT SPECIES MENTIONED

Alder	*Alnus glutinosa*
Ash	*Fraxinius excelsior*
Beech	*Fagus sylvatica*
Birch	*Betula pendula/pubescens*
Bracken	*Pteridium aquilinum*
Bramble	*Rubus* spp.
Broom	*Cytisus scoparius*
Cherry, Bird	*Prunus padus*
Gorse	*Ulex europaeus*
Hawthorn	*Crataegus monogyna*
Honeysuckle	*Lonicera periclymenum*
Juniper	*Juniperus communis*
Larch	*Larix* spp.
Larch, Japanese	*Larix kaempferi*
Myrtle, Bog	*Myrica gale*
Oak	*Quercus robur*
Pine, Lodgepole	*Pinus contorta*
Pine, Scots	*Pinus sylvestris*
Rowan	*Sorbus aucuparia*
Spruce, Norway	*Picea abies*
Spruce, Sitka	*Picea sitchensis*
Sycamore	*Acer pseudoplatanus*

[1] As in Clapham *et al* (1968)